UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ÉTUDE FONDAMENTALE ET NOUVEAUX CONCEPTS EN PALÉOLIMNOLOGIE

RECONSTITUTION À LONG TERME À PARTIR DES DIATOMÉES, DES IMPACTS PROVOQUÉS PAR LES FEUX ET LES COUPES FORESTIÈRES SUR LA BIOGÉOCHIMIE DES LACS DANS LES PROVINCES D 'ALBERTA ET DU QUÉBEC

THÈSE
PRÉSENTÉE
COMME EXIGENCE PARTIELLE
DU DOCTORAT EN BIOLOGIE

PAR
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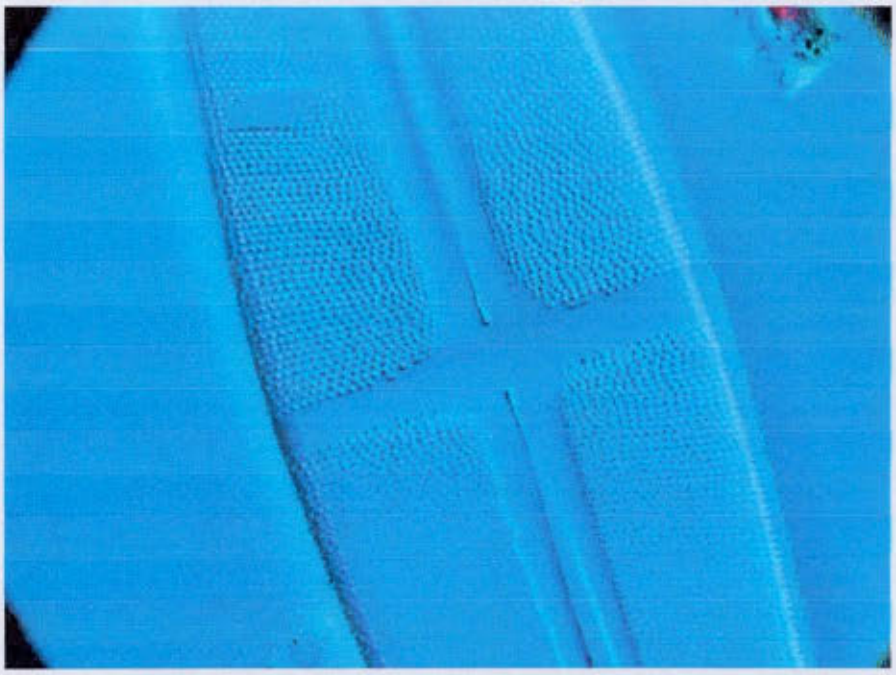
Memory of mud - in touch with tomorrow



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Résumé

L'objectif principal de ma thèse visait à quantifier, comparer et à prédire la réponse des lacs suite à différents types de perturbations (feux, coupes et climat), en vue de contribuer à l'aménagement durable de l'écosystème boréal. Pour mener à bien cette étude, j'ai examiné en détail les fondements de l'approche paléolimnologie entre autres les relations entre les espèces et les conditions environnementales. En conséquence, ma recherche incluait à la fois les aspects théoriques comme appliqués en paléolimnologie et pour une variété d'échelles à la fois spatiales et temporelles.

Au cours de mon doctorat, j'ai développé de nouvelles fonctions de transfert basées sur les diatomées à partir de variables non communément utilisées en paléolimnologie mais qui ont indéniablement une influence sur les assemblages, il s'agit de la concentration de CO_2 et de la fraction de la lumière incidente dans l'épilimnion. Afin d'améliorer le pouvoir prédictif des modèles communément utilisés en paléolimnologie, également très utiles en néo-limnologie, j'ai examiné si certaines caractéristiques des diatomées influençaient la performance de ces modèles. Premièrement, j'ai testé si les espèces planctoniques avaient un meilleur pouvoir de prédiction que les espèces benthiques étant donné que généralement les variables environnementales sont mesurées en eaux libres. Deuxièmement, j'ai comparé l'habilité des diatomées à fournir l'information aux modèles en contrôlant le nombre de taxons inclus. Ceci nous a amené à examiner le potentiel prédictif des espèces de diatomées en fonction de leur abondance, de leur nombre effectif d'occurrence (N2) ainsi que de leur tolérance. Nos résultats ont montré que même si les espèces planctoniques possédaient d'avantage d'information par individu, la grande richesse des espèces benthiques leur conférait un pouvoir prédictif bien plus important dans les modèles. Si la tolérance et le nombre effectif d'occurrence N2 ne semblaient pas influencer la performance des modèles bien qu'ayant un effet sur la racine de l'erreur quadratique, le nombre d'espèces inclues dans les modèles apparaissait comme le facteur clé. Dans la section appliquée de ma thèse, j'ai pris en considération tous les résultats de la section fondamentale, pour répondre le plus

précisément à mes objectifs. Mon étude se situe dans la forêt boréale canadienne (ouest et est canadien). L'idée générale étant d'intégrer les modèles de perturbation naturelle dans le domaine de la foresterie durable, l'aménagement est basé sur le fait que les interventions d'origine anthropique qui imitent l'intensité et la fréquence des perturbations naturelles auraient un impact minimal sur la dynamique et les processus écosystémiques en milieu terrestre comme en milieu aquatique. Par conséquent, j'ai évalué les impacts à moyen et long terme des effets uniques et cumulatifs de stresseurs multiples comme les coupes forestières ou les feux naturels, vis à vis des périodes climatiques. Cette étude a été mise en place au travers l'Alberta et le Québec en vue de comparer l'impact de telles perturbations sur des sites de caractéristiques limnologiques contrastées (géologie de surface, morphométrie, nutriments etc.). Les feux dans les forêts mixtes avaient des impacts significatifs sur les assemblages de diatomées dans les lacs en terme d'abondance relative pour les deux régions considérées, et par conséquent sur les variables chimiques reconstruites (influx de concentrations de CO_2 et de PT) quand la bonne performance des modèles le permettait. Une augmentation dans l'abondance totale et dans le rapport taxa benthiques versus planctoniques ont été observées en Alberta pendant les événements de feux, mais pas dans la richesse des espèces. En revanche les feux en forêt de conifères purs au nord du Québec n'ont pas suscité des changements apparents ou marqués dans la dynamique des assemblages de diatomées. Nous expliquons de tels résultats par la très forte humidité et la couche épaisse d'humus en sous couvert forestier qui seraient couplées avec un intervalle de feux plus long en forêt de conifères. Ceci limiterait la mobilisation des nutriments et des ions majeurs dans le bassin de drainage et implicitement dans le lac récepteur. Néanmoins je conclus que les diatomées sont un très bon indicateur de feu aussi bien pour la détection, la durée ou encore l'intensité de telles perturbations. De plus, les temps de retour à la normale sont généralement inférieurs à 1 cm de sédiment. Lorsque nous avons testé le climat comme facteur sous-jacent de la qualité des eaux dans les bassins lacustres, aucune tendance dans les assemblages de diatomées n'a été reportée pendant les deux périodes climatiques bien connues telles que la Période Médiévale Chaude « MWP » entre 800 et 1250 et Le Petit

Age Glaciaire « LIA » entre 1250 et 1850. En supposant que les prédictions climatiques sont correctes, l'intervalle des feux au Québec va augmenter et celui en Alberta diminuer. Mes résultats suggèrent alors pour le futur un moindre impact des feux en forêt mixte sur les lacs au Québec mais un impact plus important en Alberta. Si les péssières à mousses dominent encore en milieu conifériens, peu d'effet est attendu sur les lacs récepteurs. Finalement, les anciennes pratiques forestières au milieu du 20 ième siècle au Québec n'ont pas eu d'impact décelable au niveau des diatomées dans les lacs d'étude. De telles pratiques sylvicoles prévenaient probablement de fortes perturbations au niveau du sol ou de la régénération de la végétation pré établie. Les coupes forestières partielles pourraient donc être considérées comme un analogue dans les perturbations naturelles de chablis qui créent des trouées et suivent la mortalité naturelle dans les différentes cohortes.

Abstract

The overall goal of my dissertation was aimed at quantifying, comparing and predicting the response of lakes to several ecosystem-wide perturbations, which would contribute to the sustainable management of the Boreal Forest Biome (wildfires, forest harvesting and climate). In achieving this goal, however, I was also forced to examine some of the more fundamental underpinnings of the paleolimnological approach such as the inter-relationships between species and environmental variables. My dissertation research thus includes both applied and more theoretical aspects of paleolimnology at a variety of spatial and temporal scales. During my Ph.D., I developed diatom-based transfer functions from variables not commonly used in paleolimnology but which inevitably influence diatom assemblages, such as the fraction of incident light and the lake water CO_2 concentration in the epilimnion. To improve the predictive power of diatom-based transfer functions, not just with regard to paleolimnology but to other ecological issues as well, I examined whether certain characteristics of the species assemblages influenced the model performance. First, I tested whether certain types of diatoms were better at predicting lake water conditions than others (planktonic versus benthic). Second, I compared their ability to provide information to the models by controlling the number of taxa included. This led us to examine whether the "predictive" importance of diatom species within the models are a function of their effective number of occurrence or their tolerance. Our results showed that while individual planktonic species carry more predictive information than benthic ones, the vastly greater species richness of benthic types confers them a greater overall predictive power. Although the effective number of occurrence N2 and the tolerance of species influenced the stability of the model residual error, the number of species was the major factor responsible for the strength of the models. On the applied side of my dissertation, I have considered all results I found in the basic study. The study took place across the Canadian boreal forest (both eastern and western parts). The general approach was to find a way to integrate natural disturbance patterns into the framework for sustainable forestry. It was based on the principle that anthropogenic interventions that emulate the

intensity and frequency of natural disturbances will have a minimal impact on ecosystem processes and dynamics. Thus, I've attempted to assess the long-term impacts of unique or cumulative effects of multiple stressors (forest logging, wildfires and climatic periods). This was conducted both in Alberta and in Quebec, to encompass regions with greatly contrasting limnological characteristics. Forest fires in mixed-wood forests had significant impacts on diatom assemblages on both regions in term of relative abundance, and implicitly on the reconstructed biogeochemistry on lakes (pulses in CO_2 and in TP concentrations) when predictive models were reliable. In Alberta, fires induced an increase in total diatom abundance and the ratio of benthic to planktonic taxa, but did not influence species richness. In contrast, fire-induced changes in lake chemistry were small in catchments dominated by conifers in Quebec. I explained such results by the excess of moisture and the thick humus layer coupled with a longer fire interval, which likely limits the mobilization of nutrients and major ions in coniferous forests. Nevertheless, I concluded that diatoms are a good and useful indicator of fire disturbances in terms of species change for the detection, duration and magnitude of fire events, and with a recovery time inferior to the time frame of one-centimetre of sediment core. When testing the climate as an underpinning factor controlling lake water quality, no diatom assemblage changes followed the Medieval Warm Period (MWP) or the Little Ice Age (LIA) period in either regions. If the future predicted fire cycle are correct, fire interval is likely to increase in Quebec and to decrease in Alberta. My results suggest therefore a future reduced impact of mixed-wood forest fires on lakes in Quebec but an increased impact in Alberta. Finally, old selective logging techniques conducted in the winter at the mid 20^{th} century in Quebec had no detectable impact on diatom species. They should have prevented any soil and pre-established vegetative regeneration disturbances within the catchment. Selective logging could be therefore used as analogs of windthrows that create small gaps and mimic the natural mortality in undisturbed stands.

Introduction

La paléoécologie comme un outil

Une bonne compréhension de notre environnement et de ses mécanismes demande la coopération d'études sur le terrain (observations) et de la modélisation. Les études de terrain aident à définir les caractéristiques et/ou à mettre au point des théories alors que la modélisation offre une base ou une perspective théorique afin de mieux comprendre les observations. Ces deux aspects se complètent et l'un ne peut avancer sans l'autre. Tester les modèles et les confronter à la réalité est aussi un moyen d'ajuster nos connaissances, et implicitement de valider nos théories. Sans aucun doute nous appartenons à l'ère de la "prédiction". Pour des raisons purement disciplinaires les prédictions se doivent être testées et organisées pour mettre en place de nouvelles théories. Pour des raisons d'aménagement, une science prédictive est nécessaire pour inférer les coûts et les bénéfices des actions prises en aménagement et dans le but de prévenir toute dégradation environnementale (Pace 2001). Une prise de conscience du public en faveur de la protection environnementale a amené à un meilleur aménagement (Folke 1998). Outre l'objectif ultime de prédiction qu'il soit un outil en science fondamentale ou un outil en aménagement, la capacité d'inférer le présent comme le futur ne peut nous garantir avec certitude la sensibilité et l'exactitude du modèle. Par conséquent, la solution est d'intégrer la compréhension des mécanismes à des échelles à la fois temporelles et spatiales en vue d'améliorer de telles prédictions. Communément, nous prenons pour acquis l'histoire récente comme une référence fiable pour la comparaison et la prédiction même si cette dernière est largement affectée par les activités anthropiques. De plus, cette histoire récente ne peut pas prendre en compte les facteurs sous-jacents et à long terme tels que les cycles climatiques (Rhodes et Davis 1995; Fritz 1996). Les écosystèmes, en effet, peuvent aussi bien être affectés par des feux de forêt ou des tempêtes sur quelques heures, mais aussi par des coupes forestières

durant quelques semaines ou plusieurs mois, par les successions de végétation au cours des siècles ou encore les changements climatiques qui peuvent perdurer sur des millénaires. Cependant, parmi ces phénomènes "communs" ou "connus", aucun n'est aisément mesurable ou détectable à partir des expériences modernes. Par ce fait, la bonne compréhension des conditions et des changements environnementaux présents ou futurs nécessitent une ligne de base ou référence contre laquelle, les cycles climatiques ou les changements lents ou trop infréquents peuvent être comparés (Likens 1983; Schoonmaker et Foster 1991; Anderson 1995) (Figure 0.1). Les archives paléoécologiques sont un moyen pour observer dans le passé les patrons environnementaux pour une variété de cycles climatiques et de perturbations (Rhodes et Davis 1995; Fritz 1996). La paléoécologie a déjà fait ses preuves. De telles études à long terme ont fourni des données critiques sur un grand nombre de problèmes pratiques concernant la société et ont apporté également des contributions importantes à l'aménagement de l'écosystème comme au développement de nouvelles théories (Elliot 1990). Un point clé encore en paléoécologie est que cette discipline peut incorporer l'impact de facteurs multiples qui interagissent en même temps et non seulement l'impact d'un facteur unique.

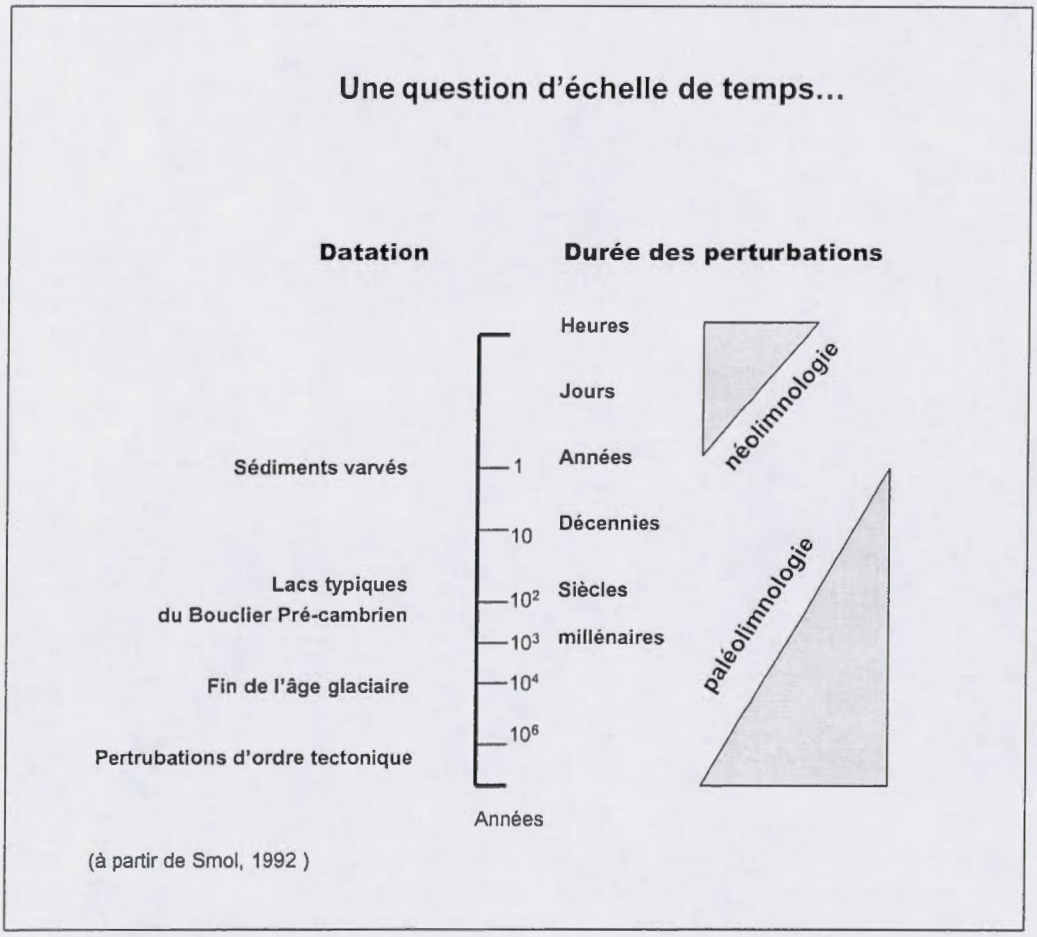


Figure 0.1 Échelle de temps néolimnologie et paléolimnologie

La paléolimnologie et ses atouts

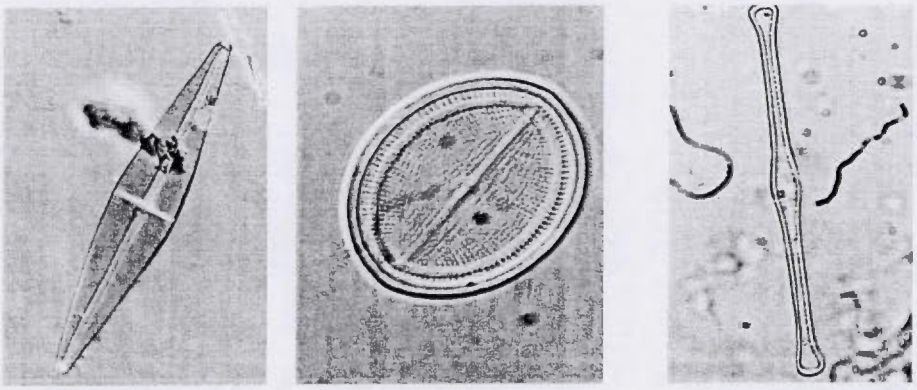
Le public et les gouvernements se sentent de plus en plus concernés par le maintien des ressources en milieu aquatique. En effet, l'écosystème aquatique boréal est reconnu comme étant un écosystème important aussi bien à buts récréatifs (baignades, pêche) que pour la conservation de la biodiversité (Kimmins 1995; Lieffers et al. 1996). Cette prise de conscience a entraîné un nouveau concept en aménagement durable de l'écosystème qui intègre à la fois les perturbations d'origine naturelles comme anthropiques. En

conséquence, la paléoécologie dans les systèmes lacustres ou paléolimnologie a pris de plus en plus d'ampleur depuis les deux dernières décennies et reste toujours en pleine effervescence. Les lacs sont, par fonction, liés aux processus géologiques, météorologiques, physiques, chimiques, et biologiques dans leur bassin de drainage terrestre comme atmosphérique (Likens et Bormann 1974). En effet, en raison des liens qui existent entre les milieux terrestres et aquatiques, toute perturbation dans le bassin de drainage qu'elle soit d'origine naturelle ou anthropique, a des effets sur les systèmes lacustres aussi bien dans leur fonction que dans leur structure (Paterson et al. 1998). L'intensité et la rapidité de la réponse des lacs aux perturbations sont régies par le système hydrologique qui affecte à la fois les apports de nutriments et les ions majeurs (Schindler et al. 1980; Bayley et al. 1992a; Fritz 1996). À partir des sédiments lacustres, la paléolimnologie est en mesure de retracer directement ou indirectement les événements passés qu'ils soient d'origine terrestre ou aquatique.

Les diatomées comme bio-indicateurs

Comme les organismes 'enregistrent' continuellement tout ce qui se passe dans leur propre environnement, leur utilisation en tant qu'indicateur écologique fournit toute l'information disponible des conditions environnementales dans lesquelles ils se trouvent. De plus, comme l'objectif principal en aménagement est en général la protection des organismes eux-mêmes, leur étude a soulevé encore plus d'intérêt (Dixit et al. 1992). Il est vrai que les organismes répondent à toutes les interactions et les impacts cumulatifs d'une multitude de facteurs. Parmi les marqueurs biologiques les plus utilisés en paléolimnologie, les diatomées sont parmi les espèces les plus utilisées pour la reconstruction des conditions environnementales passées. Par leur grande sensibilité les diatomées ont le potentiel de fournir des informations paléolimnologiques à haute résolution (Charles et Smol 1994; Moser et al. 1996; Stoermer et Smol 1999). Les diatomées sont des algues unicellulaires appartenant à la classe des *Bacillariophycea*. Elles sont composées de deux valves attachées l'une à l'autre par une ceinture qui, à elles deux, forment la frustule ou coque de nature siliceuse. Trois grands types de diatomées sont

reconnus comme suit : les Centriques, les Pennées simples et les Pénnées avec un raphé (Round 1990). Les diatomées répondent à toutes les conditions idéales comme témoin ou indicateur biologique. En premier lieu, la nature siliceuse de leur frustule (jusqu'à 70 % de silice) leur offre une très bonne conservation dans les sédiments à long terme. La forme, la taille et l'ornementation de la frustule rendent aisée l'identification des espèces vivantes et aussi fossiles (Figure 0.2). Deuxièmement, l'aptitude des diatomées à coloniser tous les milieux aquatiques ou pseudo-aquatiques (mares temporaires, suintements, boues polluées) témoigne de leur grande amplitude écologique. Il existe plus de 1000 espèces en Amérique du nord (Dixit et al. 1992). Les diatomées sont très nombreuses aussi bien en terme d'abondance totale qu'en nombre d'espèces (richesse). La rapidité de colonisation et de prolifération des diatomées, ainsi que leur stratégie de survie leur permet d'exploiter touts les types d'environnement aquatique. On les retrouve ainsi dans de nombreux types d'habitats tels que les eaux libres (planctoniques), elles peuvent être associées à des végétaux (épiphytes), les matériaux rocheux (epilithiques), le sable (épisammiques), le sédiment (épipéliques), les débris de bois (xérophiliques) ou encore accrochées aux animaux (épizootiques). En raison de leur grande sensibilité et de leur réponse rapide à tout changement dans leur environnement, les assemblages de diatomées sont même capables de révéler les changements de substances dissoutes qui sont non détectables par les moyens chimiques (Smol 1992; Smol et Douglas 1996). Partie intégrante de la chaîne alimentaire, les diatomées sont une source importante de nourriture pour leurs prédateurs et tout changement dans leur production ou leur biomasse entraîne des conséquences chez les hétéroptrophes et la fin de la chaîne alimentaire. À partir de modèles prédictifs, les assemblages de diatomées sont en mesure d'inférer quantitativement des variables environnementales qui leur sont fortement reliées directement ou indirectement. Finalement, lorsque qu'elles sont combinées aux autres études en paléoécologie (palynologie, stratigraphie des charbons, autres indicateurs), les diatomées offrent un complément d'information.



Stauroneis phoenicenteron *Cocconeis placentula* *Tabellaria flocculosa*

Figure 0.2 Photos de deux espèces benthiques *Stauroneis phoenicenteron* (140 µM longueur) et *Cocconeis placentula* (40 µM longueur) suivies par une espèce planctonique *Tabellaria flocculosa* (90 µM longueur). Ces espèces ont été échantillonnées dans les sédiments de surface de l'ensemble de calibration moderne au Québec.

Techniques d'échantillonnage et de laboratoire

Analyse des diatomées

Afin de reconstruire les variables limnologiques à partir des diatomées fossiles, un ensemble de calibration moderne doit être préalablement complété pour établir les relations quantitatives entre les assemblages de diatomées modernes et les variables environnementales actuelles. En premier lieu, les conditions climatiques, géographiques, géologiques, topographiques, physico-chimiques sont mesurées selon des méthodes standards directement sur le terrain ou au laboratoire. Deuxièmement, les sédiments de surface contenant les diatomées modernes sont échantillonnés. La préparation et l'analyse des échantillons de diatomées suivent des procédures communément utilisées (Figure 0.3). Brièvement, les échantillons de sédiment séché sont placés dans une solution d'acide chlorhydrique (HCl) afin de dissoudre les carbonates. Des acides forts

(H_2O_2 ou le mélange royal HNO_3 et H_2SO_4) sont ensuite ajoutés pour digérer la matière organique (Battarbee 1973, 1986; Wilson 1996). La digestion peut se poursuivre durant plusieurs jours. Afin d'accélérer la réaction, les échantillons sont placés dans un bain-marie pendant au moins deux heures. Les étapes de centrifugation et rinçage à l'eau distillée sont répétées jusqu'à ce que les échantillons soient dépourvus d'acide. Le matériel siliceux récupéré dans le culot des tubes est ensuite séché sur des lamelles et puis monté sur lames à l'aide d'une résine (naphrax). Pour chaque lame, un minimum de 500 valves de diatomées est identifié à un taux d'amplification de 1600 fois suivant des transects au hasard. L'abondance totale des valves de diatomées par gramme de sédiment est évaluée à l'aide d'une solution standard et calibrée de *Eucalyptus globulus* (Fægri et al 1989). La même méthode est employée aussi bien pour les diatomées de surface que celles collectées en profondeur dans les carottes des sédiments. La taxonomie est basée sur Hustedt (1930-1966); Krammer et Lange-Bertalot (1986-1991), The PIRLA Diatom Iconography (Camburn et al. 1984-1986) et Fallu et al. (2000).

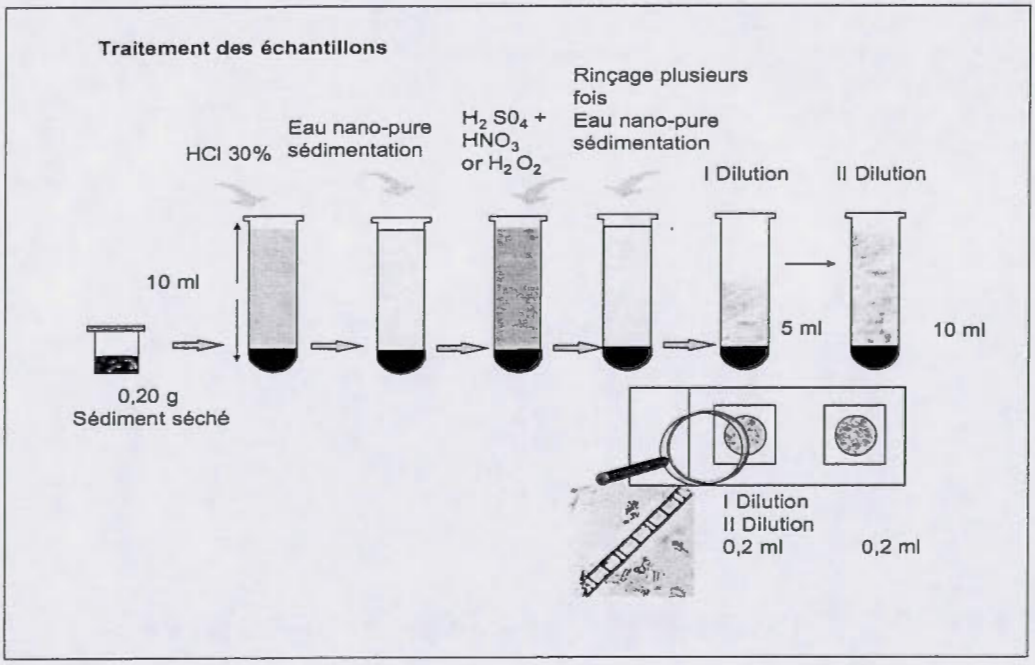
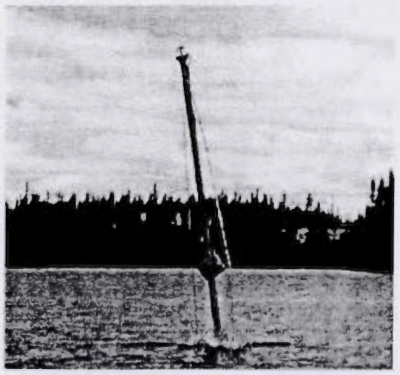


Figure 0.3 Étapes de préparation pour l'extraction et l'identification des diatomées

Extraction et datation des carottes de sédiment

Plusieurs types de carottiers sont utilisés selon la longueur de carotte. Si le carottier Kajak-Brinkhurst (KB) est souvent utilisé pour des périodes courtes (quelques centaines d'années en général) ou les sédiments de surface, le carottier McKereth avec ses 6 mètres de sédiment peut retourner à plusieurs milliers d'années (Figure 0.4). Ayant pour objectif de déterminer la datation des profils sédimentaires, une variété d'approches est disponible telles que les isotopes. La chronologie peut être basée sur AMS ^{14}C et ^{210}Pb, mais aussi à partir des profils de ^{137}Cs. Les stratigraphies de charbon sont couramment utilisées pour retracer les événements de feux. Lorsque les carottes de sédiments sont laminées de manière continue, il est même possible, en comptant le nombre de varves, d'estimer les ages en complément toutefois des techniques précédentes.

Carottier
Kajak-Brinkhurst (KB)



Carottier McKereth

Figure 0.4 Photos de deux carottiers pour extraire nos sédiments en surface comme en profondeur

Analyse statistique

Si depuis une vingtaine d'années il y a eu des avancées en technologie pour le découpage des carottes, la microscopie, les collections de flores (Renberg 1981; Glew 1988; Smol 1992; Birks 1994) et les méthodes chronologiques (MacDonald et al. 1991) ; les plus grands progrès se sont faits en modélisation (ter Braak et van Dam 1989; Birks et al. 1990a; ter Braak et Juggings 1993). La paléolimnologie est passée d'une science qualitative et descriptive vers une science quantitative et numérique (Birks 1998).

L'approche statistique est composée de deux étapes principales, la calibration suivie de la régression (Figure 0.5). La première étape a pour but d'évaluer les relations existantes entre l'abondance relative des espèces de diatomées modernes (surface de sédiment représentant les deux à trois dernières années) et les variables environnementales actuelles. Une fois que la ou les variable(s) plus fortement corrélées sont identifiées, les modèles de prédiction ou fonctions de transfert peuvent être développés dans une seconde étape (étape de régression). Deux types de modélisation sont utilisés dans cette présente thèse, la première est celle des modèles de moyenne pondérée des moindres carrés partiels « WA-PLS » (ter Braak et Juggins 1993), alors que la seconde approche utilise les réseaux de neurones artificiels « ANN » basés sur un algorithme de gradient rétro-actif ou « back-propagation » (Rumelhart et al. 1986). Cette dernière technique a été récemment proposée en paléolimnologie par Racca et al. (2001).

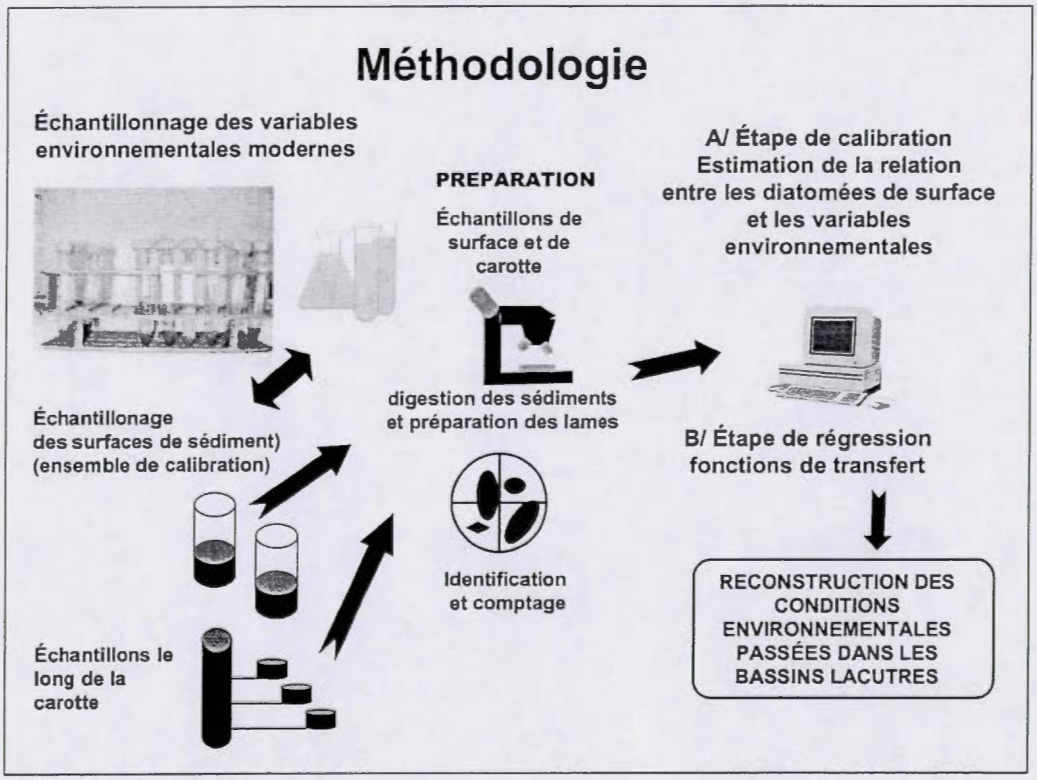


Figure 0.5 Étapes majeures de la méthodologie générale en paléolimnologie

Contexte de l'étude

Dans les forêts boréales canadiennes au Québec et en Alberta, les feux sont les agents de perturbation naturelle majeurs (Rowe et Scotter 1973). Si les prédictions climatiques sont correctes, le cycle de feux des forêts tend à diminuer dans l'est canadien (Bergeron et Archambault 1991; Carcaillet et al. 2001a) mais aurait tendance à augmenter en Ontario et dans l'ouest canadien (Schindler et al. 1996a; Schindler 1998; Flannigan et al. 1998, 2001). Les coupes forestières représentent actuellement la principale cause de déforestation et visent encore à s'accroître en raison des demandes mondiales qui supportent cette économie fructueuse. La politique d'aménagement à long terme est d'adapter les pratiques sylvicoles pour concilier à la fois les coûts de production de bois

avec la productivité des forêts ainsi que la biodiversité (Attiwil 1994; CCFM 1995). Ce consensus implique l'intégrité des processus écologiques et de la dynamique des écosystèmes aussi bien terrestres qu'aquatiques (CCFM 1995). L'aménagement durable est basé sur la conception suivante: tout organisme et par extension l'écosystème-capable de supporter des perturbations naturelles de faible ou de grande ampleur (exemples : feux de forêt, épidémies d'insectes, tempêtes) sont probablement adaptés aux perturbations d'origine anthropique tant et si bien que ces dernières sont comparables en fréquence et en intensité aux perturbations naturelles (Bergeron et al. 1999). L'approche générale est d'intégrer les patrons de perturbations naturelles dans un réseau de foresterie durable. Le principe est le suivant: les interventions d'origine anthropique qui imitent le mieux les perturbations d'origine naturelle auraient un minimum d'impact sur la dynamique et les processus des systèmes terrestres comme aquatiques. Alors que les coupes à blanc sont considérées comme ayant des impacts similaires à ceux des feux, les coupes partielles auraient les mêmes effets que les chablis (trouées dans une cohorte d'arbres) (Johnson 1998; Bergeron et al. 2000). Bien que l'analogie entre l'aménagement forestier et les perturbations naturelles en écosystème boréal ait des mérites (Bergeron et al. 1999), il reste cependant quelques points à éclaircir en raison du manque de connaissances de la dynamique et du fonctionnement de l'écosystème boréal.

Objectifs principaux de la thèse

Une attention particulière repose sur l'établissement d'outils capables d'estimer les impacts à long terme des pratiques sylvicoles, en comparaison avec les perturbations naturelles sur la biogéochimie des lacs à partir des restes de diatomées. Le but général de la thèse est de quantifier, comparer et prédire les réponses des lacs aux différents types de perturbations (feux, coupes tous deux associés au climat) afin de mieux contribuer à l'aménagement durable de l'écosystème boréal. Pour améliorer la sensibilité et la précision des reconstructions à partir des modèles j'ai été amenée à examiner, en premier lieu, les principes et les fondements de l'approche paléolimnologique qui sont basés sur les relations entre les espèces de diatomées et les variables environnementales.

Structure de la thèse

La thèse est constituée de deux grandes parties, la première est fondamentale et la seconde est appliquée aux besoins d'aménagement en territoire boréal, toutes deux établies sur différentes échelles spatiales comme et temporelles.

Approche fondamentale et théorique. Un nouveau défi.

La paléolimnologie est une nouvelle discipline en continuelle expansion, cependant il est encore difficile d'identifier toutes les nouvelles découvertes et théories développées jusqu'à présent. Néanmoins, le développement et le raffinement de certains fondements ou principes méritent davantage d'intérêt et de sollicitude. Je me suis donc exercée à développer de nouveaux modèles à partir de variables non communément utilisées et à améliorer la performance de ces modèles en cherchant quelle en était la source.

Chapitre I- Fonctions de transfert basées sur les diatomées dans les lacs de l'ouest Québecois (Abitibi et Haute Mauricie): le possible rôle du CO_2 dans la distribution des diatomées.

N'y a-t-il pas une variable non communément utilisée en paléolimnologie qui pourrait influencer les assemblages de diatomées? À cette fin, des fonctions de transfert ont été développées à partir de nouvelles variables comme la fraction de la lumière incidente et la concentration de CO_2 dans l'épilimnion qui indéniablement influencent les communautés diatomiques.

Chapitre II- Est-ce que l'introduction d'espèces benthiques est-elle nécessaire pour la reconstruction des conditions environnementales en eaux libres à partir des fonctions de transfert?

Est-ce que l'utilisation de toutes les diatomées (planctoniques et benthiques) est nécessaire pour l'élaboration de modèles prédictifs performants et significatifs? Y aurait-il d'autres facteurs qui contrôleraient la performance des modèles et lesquels? Afin d'améliorer le pouvoir prédictif des fonctions de transfert basées sur les diatomées, et

ceci, pas juste au regard de la paléolimnologie mais aussi envers d'autres études en écologie, j'ai examiné les caractéristiques des espèces en détail. En premier lieu, des tests ont été réalisés afin de déterminer quel type de taxa (planctoniques, benthiques ou les deux ensemble) offrait la meilleure performance des modèles. Deuxièmement, en contrôlant le nombre d'espèces inclues dans chaque modèle, j'ai comparé leur aptitude à rapporter l'information dans les modèles. Cette approche m'a conduit par la suite à tenir compte d'autres facteurs propres aux espèces dans la performance des modèles comme le nombre effectif d'occurrence ou N2 ainsi que la tolérance des espèces.

Approche appliquée

Mon projet s'intègre dans un projet commun du Réseau du Centre d'Excellence de la Gestion Durable des Forêts (RCE-GDF). L'approche générale du RCE-GDF est que les perturbations naturelles puissent être intégrées en foresterie durable. Le paradigme se résume comme suivant : mise en place d'un aménagement durable à partir de la simulation des perturbations naturelles, pour la mise en place de nouvelles pratiques sylvicoles et diminuer ainsi les impacts d'origine anthropique dans les systèmes terrestres et lacustres. Dans la partie appliquée de ma thèse j'ai considéré tous les résultats de la section fondamentale. Mon étude prend place dans le biome boréal de l'ouest canadien en Alberta mais aussi dans l'est au Québec. Même si l'historique des coupes est plus ancien au Québec (1910) et a bénéficié d'une étude paléolimnologique, un historique à long terme des feux de forêt dans les deux provinces m'a permis de retracer les impacts sur un à plusieurs milliers d'années.

Chapitre III-les 1000 dernières années de périodes de feux et de changements climatiques : effets des changements sur les diatomées de Christina Lake.

L'impact des feux de forêt sur Christina Lake a été étudié à partir d'une étude paléolimnologique en région forestière boréale mixte de l'ouest canadien au nord de l'Alberta. En raison du peu d'études à long terme réalisées dans les systèmes dominés par les forêts entourées de marécages, j'ai utilisé les diatomées pour reconstruire les

conditions environnementales passées de la chimie de l'eau. Cette étude a bénéficié de la reconstitution historique des feux à partir d'une étude similaire faite sur la stratigraphie des charbons (Laird et Campbell 2000). Mon premier objectif visait à savoir si lors d'un feu, l'abondance totale des espèces tendait à croître et ou la richesse des espèces diminuait comme préalablement observé dans une autre étude mais au Québec (Enache et Prairie 2000). En second lieu, j'ai testé si le rapport des taxa benthiques versus taxa planctoniques était influencé par l'apport des particules de charbon suite à un feu, étant donné la faible tolérance des taxa planctoniques aux faibles conditions lumineuses. Finalement, j'ai également testé si les changements dans les assemblages de diatomées suivaient les différentes périodes climatiques comme la Période Médiévale Chaude « MWP » et le Petit Age Glaciaire « LIA ».

Chapitre IV- Les tendances à long terme des concentrations en CO_2 dissous dans l'épilimnion à partir des restes de diatomées dans un petit lac de culot de fonte de glace au Québec (Abitibi): impacts des feux de forêt.

Dans ce chapitre je reconstruis les concentrations en CO_2 dissous dans l'épilimnion du Lac Francis, un petit lac de culot de fonte de glace, typique de l'écorégion de la ceinture d'argile en Abitibi (Québec). Cette reconstruction a bénéficié de l'historique des feux à partir de la stratigraphie des charbons développée dans une autre étude (Carcaillet et al. 2001a, b) et ceci pour les 8000 dernières années. J'ai cherché à déterminer si les feux influençaient les concentrations en CO_2 dissous et si oui, sur quelle période de temps. Je me suis aussi intéressée aux tendances temporelles le long de la carotte sédimentaire de ces mêmes concentrations de CO_2 et si elles reproduisaient directement la fréquence des feux. J'ai également examiné si les changements dans les assemblages de diatomées répondaient aux différentes périodes climatiques comme la Période Médiévale Chaude « MWP » et le Petit Age Glaciaire « LIA », mais aussi s'il existait une relation avec la variation de la composition forestière dans le bassin versant.

Chapitre V- Étude paléolimnologique de 1200 ans dans un petit lac de culot de fonte de glace dans le domaine de l'épinette moire à mousses (Québec, Canada) : impact des feux sur la biogéochimie du lac à la Pessière à partir des restes de diatomées.

En raison des différences importantes dans la succession de végétation après feu entre des forêts mixtes et à dominance de conifères déjà observées au Québec, et due à la relation entre milieu terrestre et aquatique, j'ai mené une reconstruction paléoécologique à long terme des impacts des feux sur la biogéochimie du Lac à la Pessière appartenant au domaine de forêt de pures conifères. Nos résultats ont été comparés avec des études réalisées en forêt mixte plus au sud (chapitre IV lac Francis). L'étude paléolimnologique a été réalisée à partir de restes de diatomées afin de reconstruire pour les derniers 1200 ans, les changements environnementaux d'intérêt limnologique (pH, phosphore total (PT), azote total (NT), carbone organique dissous (COD) et la concentration en dioxyde de carbone dans l'épilimnion (CO_2)). J'ai comparé la composition des diatomées et les variables reconstruites avant et après perturbation de feu. J'ai aussi comparé les résultats observés après perturbation en forêt de conifères avec ceux observés en forêts mixtes (chapitres III et IV) (Enache et Prairie 2000 ; Philibert et al. soumis).

Chapitre VI- Impact des coupes de forêt de la moitié du vingtième siècle sur la biogéochimie des lac en Haute Mauricie (Québec, Canada) inférés à partir des restes de diatomées : implications en aménagement durable de l'écosystème boréal.

Je me suis intéressée à l'impact des coupes forestières partielles entre 1935 et 1960 sur la biogéochimie de trois lacs en Haute Mauricie (Québec, Canada) dans le domaine forestier boréal mixte. Dans le bassin versant 60 à 80 % du territoire forestier avait été coupé progressivement sur quelques années (5 à 10 ans) et durant la période hivernale. J'ai fait une étude paléolimnologique en vue de reconstruire l'amplitude des impacts des coupes sur les pertes de nutriments du bassin versant et la biomasse totale des diatomées, et de comparer ces impacts avec des études modernes réalisées dans la même

région mais sur ces coupes totales ou à blanc (Carignan et al. 2000; Planas et al. 2000). J'ai utilisé encore une fois les diatomées comme indicateur de changement des conditions environnementales après coupes pour les variables qui nous intéressaient comme pH, TP, TN, et DOC.

La conclusion générale porte sur les différents résultats de la présente thèse ainsi que les perspectives futures suite à cette étude.

J'ai aussi participé à la comparaison du pouvoir prédictif de modèles couramment utilisés en paléolimnologie ou moyenne pondérée des moindres carrés partiels « WA-PLS » avec les réseaux de neurones artificiels « ANN » dans l'annexe de la thèse (Racca et al. 2001).

En annexe également, les listes des flores de diatomées rencontrées au Québec et en Alberta dans les ensembles de calibration modernes sont disponibles avec, pour chaque taxon ses caractéristiques écologiques.

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Introduction

Paleoecology as a tool

It is widely recognized that understanding our environment and its mechanisms requires the co-operative effort of field studies (observations) and modelling. The field studies helps to define the characteristics and/or build up theories and the modeling provides a theoretical basis and perspective for understanding the observations. Both work together and one cannot advance without the other. Testing the models and confronting them to reality is also to assess the adequacy of our understanding and further the validity of our theories. We undoubtedly belong to the era of "prediction". For purely disciplinary reasons there is a need for predictions to test, organize, and submit new ideas or theories. For management, a predictive science is needed to forecast the consequences costs, and benefits of management actions to forestall some of the worst environmental degradation that the future appears to hold (Pace 2001). Since a couple of years strong public sentiments for environmental protection have promoted better ecosystem management (Folke 1998). Regardless the aim of the prediction seen as a fundamental or management tool, the ability to simulate the present or the foreseeable environment could not guarantee that the modeled environment sensitivity is accurate. Therefore, the challenge remains to integrate understanding of mechanisms at various temporal and spatial scales for enhancing predictions. Commonly we take the recent history as a reference for comparison or prediction even if greatly altered by anthropogenic activities and without taking in consideration underpinning long-term factors such as climatic cycles (Fritz 1996). Ecosystems may be affected by catastrophic forest fires and windstorms lasting hours, by timber harvesting lasting weeks or months, by forest succession lasting centuries, and by climatic changes lasting millennia but none of these common phenomena is amenable to direct measurement or experimentation (Smol 1992) (Figure 0.1). By this fact, discussion of the nature of the modern or future

environmental conditions and changes necessitate a baseline or long-term natural time series against which different disturbances, climatic cycles, and infrequent or too slow ecosystemic changes and natural variability can be compared (Likens 1983; Schoonmaker and Foster 1991; Anderson 1995). Paleorecords are a tool for looking at environmental patterns and show a range of climatic and disturbance states far greater than those documented by written records (Rhodes and Davis 1995; Fritz 1996).

Paleoecology has already proven useful since the modern natural or anthropogenic-originated disturbances and global warming have got their potential analogs during the quaternary period (the Holocene). Such long-term investigations have provided critical data on a number of practical issues that are of concern to society and have made important contributions to the ecosystem management and the development and testing of ecological theory for understanding the global system (Elliott 1990). A final key point in paleoecological record is that multiple factors affect biota in ways not easily predicted from the effects of single factors considered alone.

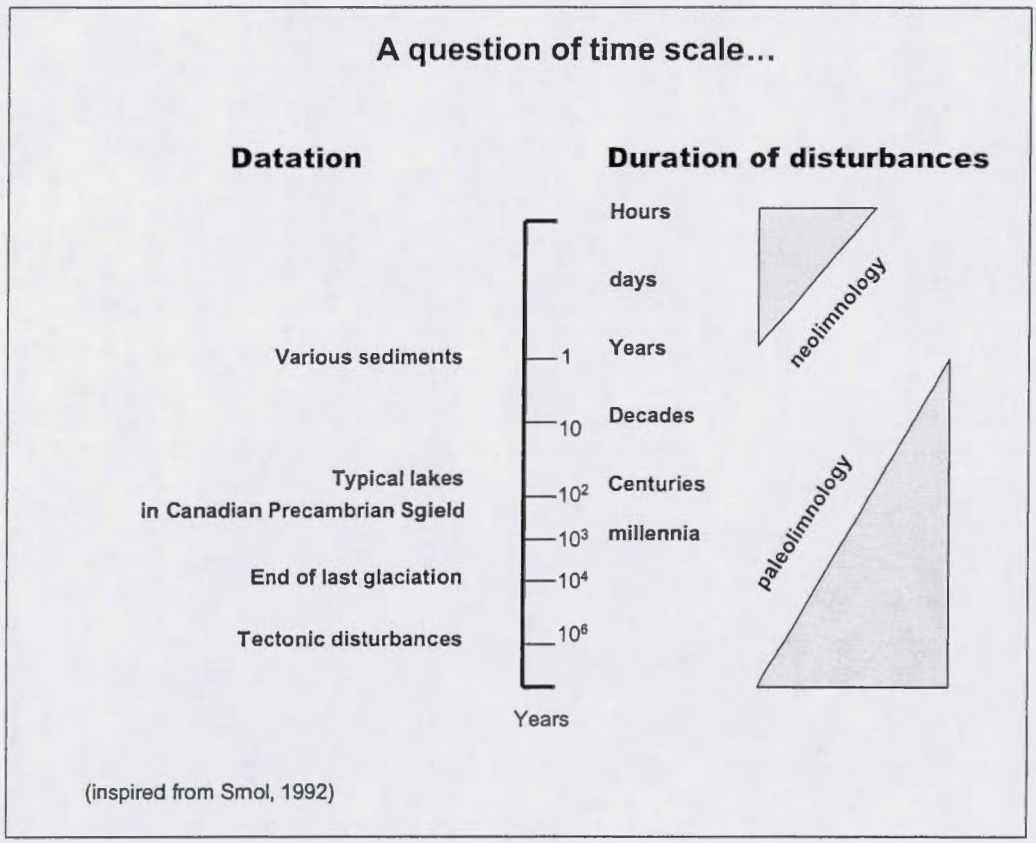

Figure 0.1 Time scale in neolimnology and paleolimnology.

Paleolimnology concern

The public and consequently the governments are becoming increasingly concerned with maintaining aquatic resources. Indeed, boreal ecosystem is increasingly viewed as an important ecosystem for wildlife, recreation and biodiversity conservation (Kimmins 1995; Lieffers et al. 1996). This awareness has resulted in a concept of sustainable ecosystem management that integrates both natural and human disturbances. As a consequence, paleoecology in lake systems; or so-called paleolimnology, has been of growing concern and is still being in an active area of research. Any disturbance within the catchment may influence the lakes into which they drain. Lakes are functionally linked to geological, meteorological, physical, chemical and biological processes within

their watershed and their airsheds (Likens and Bormann 1974). Indeed, because of terrestrial-aquatic linkages, any disturbance in the watershed alters lacustrine systems in a number of ways in both their structure and function (Paterson et al. 1998). The magnitude and the rate of lacustrine responses are mediated by the hydrologic mass balance that can alter both mineral and nutrient inputs into aquatic systems (Schindler et al. 1980; Bayley et al. 1992a; Fritz 1996).

Diatom as bio-indicators

Because aquatic organisms monitor continuously their own environment, the use of biota directly provides the most information on changing conditions (Dixit et al. 1992). In addition biota respond to the interaction and cumulative impacts of a variety of factors or habitat characteristics which could not be interpreted individually by chemical or physical samples. Among the bio-indicators in paleolimnology, diatoms are the most widely used and sensitive indicators of past changes in lake environment (Moser et al. 1996; Stoermer and Smol 1999) (Figure 0.2). Diatoms are single-cell algae belonging to the class of *Bacillariophyceae*. Primarily composed of silicates (SiO_2), they are made of two valves (one frustule) belted with girdle bands. Three main types of diatom morphology are recognized such as the centric, simple pennates and raphid pennates (Round et al. 1990). Diatoms respond to the pre-required ideal conditions as biological indicators as following. First, their silicate nature permits to them to be very well preserved in lake sediments for at least a couple millennia and the frustule's shape and ornamentation are helpful to identify them and do not vary between alive or dead individuals. Second, they are broadly distributed worldwide in lakes but as well in oceans, wetlands, rivers and soils and are very numerous (more than 1000 taxa in North of America (Dixit et al. 1992). They are also numerous in all aquatic systems in term of abundance and number of species. Ecologically diverse, diatoms inhabit all types of habitats such as in the open-waters (planktonic), associated with plants (epiphytes), rocks, (epilithon), sand (episammon), mud (epipelon) woods (xerophilic) and animals (epizootic). Due to their high sensitivity and their quick response, diatom assemblages can reveal quick changes

and in factors (dissolved chemicals) which are not detectable from chemical means and provide paleolimnological data with high resolution (Smol 1992). These assemblages can infer quantitatively environmental variables that are strongly directly or indirectly correlated to them by their optimas and their tolerance to each variable (Smol and Douglas 1996). Due to the intra and/or inter-competition, shifts in diatom abundances can be observed. At the base of the food web, shifts in diatom assemblages can also be a consequence of predation but are of prime importance for the rest of the food web. Eventually, the diatom analysis in sediment cores can be joined to other bioindicators such as cladocera, Ostracoda, chironomids, chrysophytes, pigments, but also coupled with disciplines such as palynology and geochemical and charcoal data.

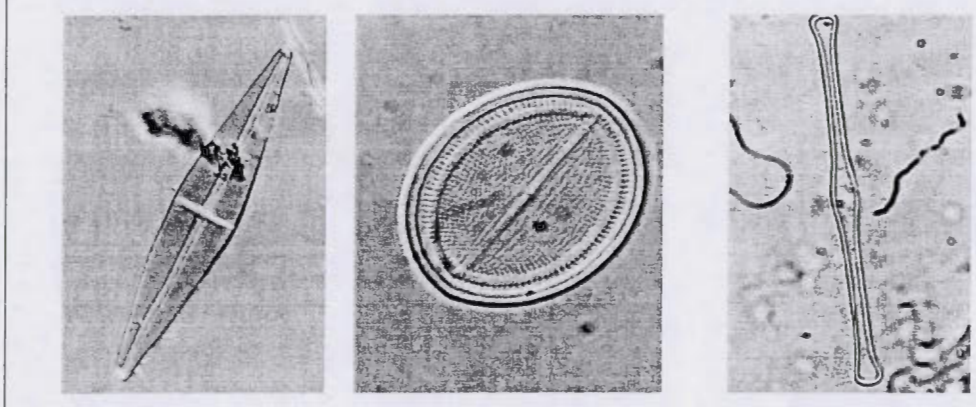

Figure 0.2 Pictures of two benthic species *Stauroneis phoenicenteron* (140 µM length) and *Cocconeis placentula* (40 µM length) followed by one planktonic *Tabellaria flocculosa* (90 µM length).
All these species were collected from surficial sediments in the modern calibration set in Quebec.

Field and laboratory techniques

Diatom analysis

Accurate estimates of past environmental conditions are based on biological assemblages and assume that we can statistically model the present-day responses of species in relation to the environmental conditions under which species live (Wilson et al. 1996). Quantitative paleo-methods all are based on a surface sediment training set consisted of a number of lakes that cover a diverse range of limnological conditions, and biotic assemblages preserved in surface sediments (integrated samples in space and in time that represent the last few years) (Wilson et al. 1996). To reconstruct the limnological variables from diatom fossils a modern calibration set is completed in order to establish the quantitative relationships between the modern diatom assemblages and the actual environmental data. First, modern water, geographical, topographical, climatic, physical and chemical data are measured following standard procedures directly in the filed or in the laboratory. Second, surface sediments representing the last few years of deposit are collected from the modern calibration set and contain "modern" diatoms. The preparation and analysis of diatom samples follow standard techniques (Figure 0.3). The same protocol is used for the extraction, identification and counting of fossil "diatoms". Briefly, dried sediment samples are placed in a solution of hydrochloric acid (HCl) in order to dissolve carbonates. Strong acids (H_2O_2 or a mixing of HNO_3 and H_2SO_4) are added to digest organic material (Battarbee, 1973, 1986 (H_2O_2) and Wilson et al. 1996 (HNO_3 and H_2SO_4). The digestion can proceed over several days. To accelerate the reaction samples are placed in a boiling water bath for two hours at the end of the digestion process. The centrifuging/washing step is repeated until the samples are acid-free. The resulted siliceous material is dried on coverslips and subsequently mounted on slides by a resin (naphrax). For each sample a minimum of 500 diatom valves is counted and identified along random transects at a magnification of 1600x. The total abundance of diatom valves per gram of oven dried sediment in each interval is evaluated using a standardized solution of *Eucalyptus globulus* pollen ground. The same methods for diatom

analysis are used for surface and deep core samples. Taxonomic identification of diatoms was based on Hustedt (1930-1966); Krammer and Lange-Bertalot (1986-1991), The PIRLA Diatom Iconograph (Camburn et al. 1984-1986) and Fallu et al. (2000).

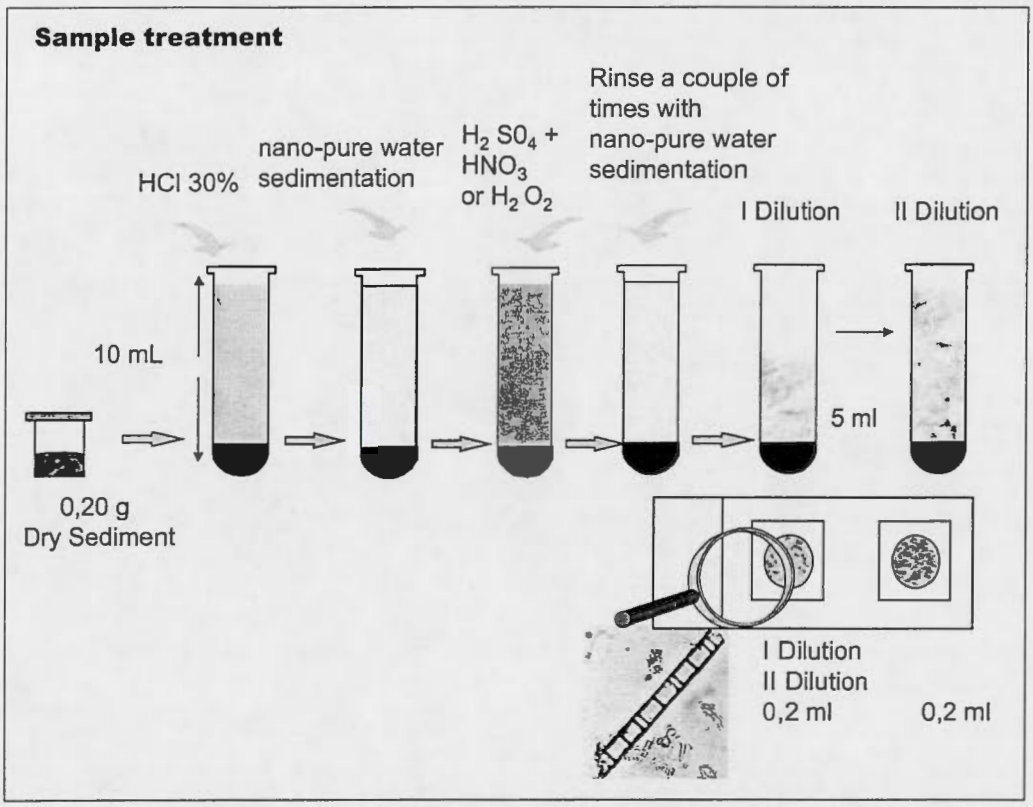

Figure 0.3 Different steps for extraction and identification of diatom samples

Extraction and dating of cores

Whereas a Kajak-Brinkhurst (KB) gravity corer is used commonly used to collect the surface sediment, a McKereth sampler with 6-m length was utilized to sample the entire sediment core from the deepest portion of lakes (Figure 0.4). The two cores were sliced into centimetre sections. At each section, 1 cm^3 sample was taken along the longitudinal

Axis of the core for charcoal tallying. Pollen and diatom analyses were carried out at each cm. In order to determine the depth time relative of sediment cores, a variety of approaches can be used, such as "isotopic clocks" (Dixit et al. 1992). The chronology can be based on accelerator (AMS) ^{14}C feasible for milligram quantities of carbon that has permitted the dating of terrestrial plant macrofossil from lake sediments, thereby avoiding the "old carbon effect" associated with whole sediment containing remains of aquatic biota. Radiometric ^{210}Pb dating is limited to the past ca. 125 years. Markers in the past few decades are also markers for atomic bomb testing in the atmosphere such as ^{137}Cs decay profiles. Chronostratigraphic markers as charcoal can be associated with known fires. When the basin contains continuously laminated sediments sediment age can be estimated by varve counting in addition of isotopic techniques.

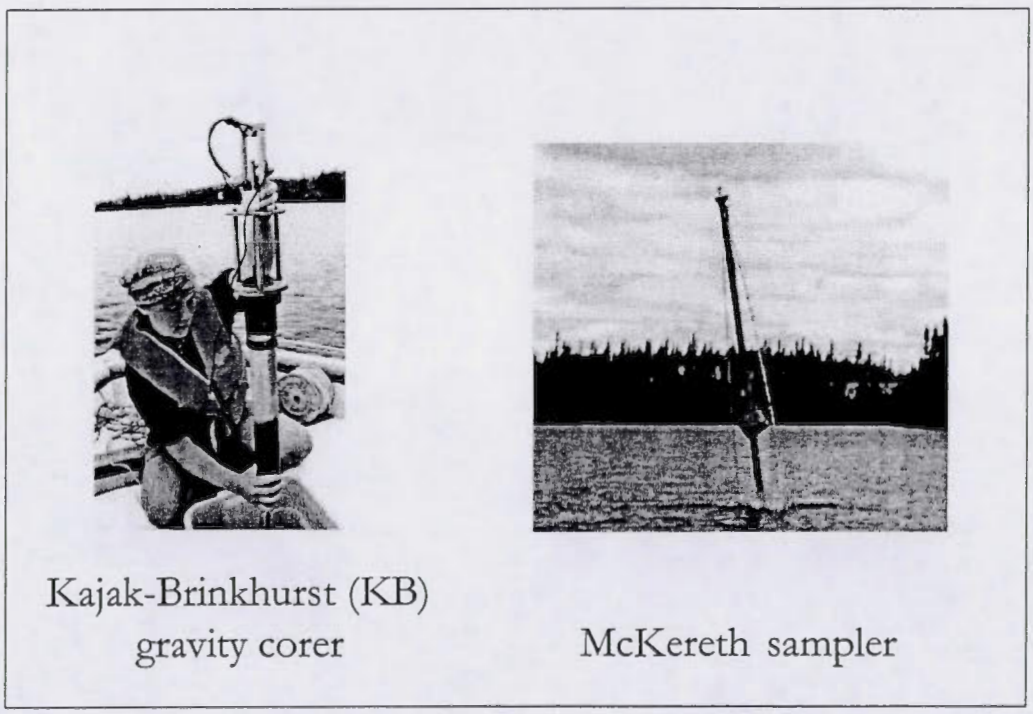

Figure 0.4 Pictures of two corers for the extraction of surficial or downcore sediment samples

Statistical analysis

Since the last 20 years, developments in applied statistical approaches have grown at a rapid rate in paleolimnology. In addition to technological advances made in collections, in improved microscopy, in sectioning (Renberg 1981; Glew 1988; Smol 1992; Birks 1994), in chronological techniques (MacDonald et al. 1991), much progress has been made in statistical modelling (Wold et al. 1984, ter Braak and van Dam 1989; Birks et al. 1990a; ter Braak and Juggings 1993). Methods have shifted from being qualitative and descriptive to become quantitative and analytic (Birks 1998). This new potential has offered to paleolimnology to be reliable when addressing environmental questions and hypotheses, concerning the impacts of environmental changes on lacustrine systems. The statistical approach is composed of two main steps, calibration and regression (general methodology in Figure 0.5). The first one aims at assessing the relation between the relative abundance of modern diatoms and actual environmental variables. Once the most strongly correlated environmental variable to diatom assemblages are identified, predictive models can be developed (regression step). Two types of modelling methods are utilised in this dissertation. One commonly used method is Weighted Averaging Partial Least Squares (WA-PLS) (ter Braak and Juggins 1993), whereas the second using artificial neuronal networks (ANN) based on the back-propagation algorithm (Rumelhart et al. 1986) have been recently proposed by Racca et al. (2001) in paleolimnological studies.

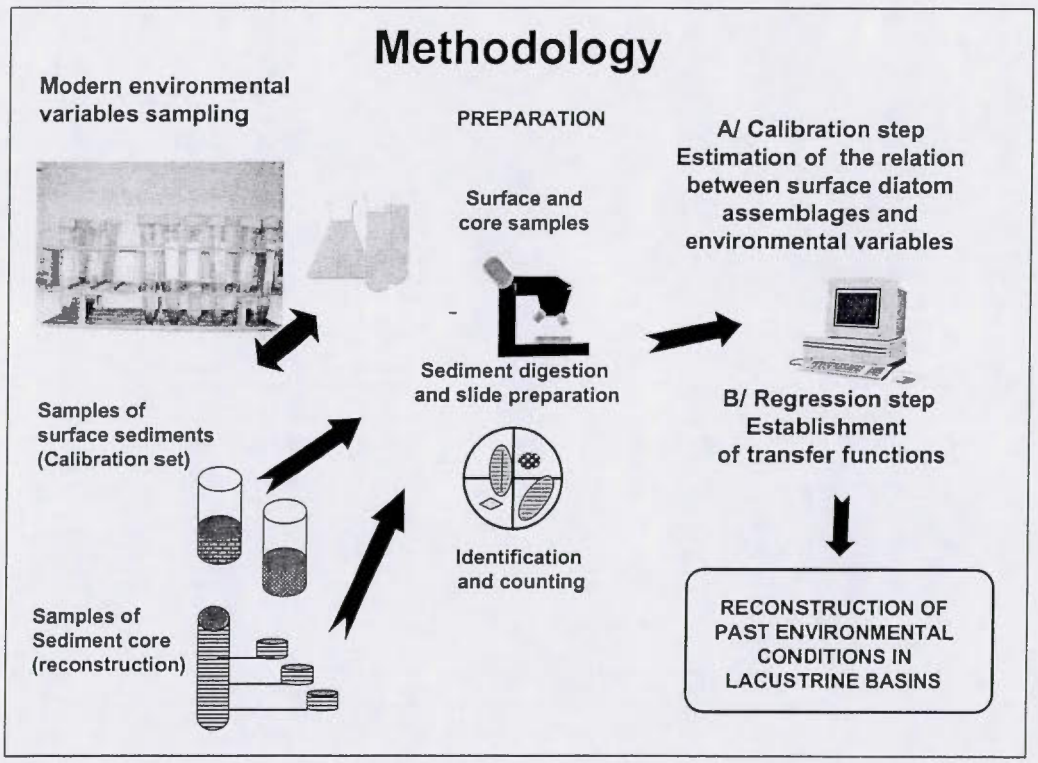

Figure 0.5 Main steps of the general methodology in paleolimnology

Context of the main study

In the boreal forests of Canada, wildfires are among the most important natural disturbances. If climatic forecasts are correct, the forest fire cycle is likely to decrease in the eastern part of Canada (Bergeron and Archambault 1991; Carcaillet et al. 2001a) but increase in Ontario, as well as in the Boreal Plain in the Prairies (Schindler et al. 1996; Schindler 1998; Flannigan et al. 1998, 2001). Forest cutting for wood production (timber and firewood) is one of the principal causes of deforestation and is going on according to world demand in industrial and energy business needs. Today a growing concern is to adapt silvicultural practices to conciliate both cost-effective wood production and the integrity of natural ecological dynamics and processes of the boreal biome under a sustainable management policy (Attiwil 1994; CCFM 1995). This implies that the

integrity of ecological processes in forest and aquatic ecosystems must be maintained (CCFM 1995). This fact leads to the following conception: an organism- and by extension an ecosystem - capable of withstanding large natural perturbations (e.g. wildfires, insect epidemics, and storms) are probably "adapted" to withstand human perturbations of comparable magnitude and frequency (Bergeron et al. 1999). Because timber harvesting (clear-cutting) is considered to have similar effects to those of natural disturbances such as wildfire and partial logging to those of insect outbreaks or windthrows (Johnson et al. 1998; Bergeron et al. 2000), it was based on the principle that anthropogenic interventions that emulate the intensity and frequency of natural disturbances will have a minimal impact on terrestrial and aquatic system processes and dynamics. Although the analogy between forest management and fire disturbance in boreal ecosystems has some merit (Bergeron et al. 1999), it is important to recognize that it also has some limitations related to the limited knowledge of the dynamics and functioning of the boreal ecosystem.

Main objectives of the study

The overall goal of my dissertation was aimed at quantifying, comparing and predicting the response of lakes to several ecosystem-wide perturbations from diatom remains, which would contribute to the sustainable management of the Boreal Forest Biome (wildfires, forest harvesting and climate).

Due to the fact that much work has to be done before paleolimnology can be fully capable of testing the sensitivity and accuracy of the predictive models, in achieving this goal, I was forced to examine some of the more fundamental underpinnings of the paleolimnological approach such as the inter-relationships between species and environmental variables. My dissertation research thus includes both applied and more theoretical aspects of paleolimnology at a variety of spatial and temporal scales.

Thesis structure

Two main sections are approached. My dissertation research thus includes both applied and more theoretical aspects of paleolimnology at a variety of spatial and temporal scales.

Fundamental and theoretical approach. A new challenge

Paleolimnology is a new interdisciplinary science that continues to expand. It therefore remains difficult to identify new discoveries and innovations in such a recent development. Nevertheless I still believe that the development of some principles or underpinnings deserve more much growing interest and solicitude. Therefore I developed new transfer functions from variables not commonly used and explore what factor(s) was responsible for the performance in the models.

Chapter I-Diatom-based transfer functions in western Quebec lakes (Abitibi and Haute Mauricie): the possible role of epilimnetic CO_2 concentration in influencing diatom assemblages

Is there any variable not commonly used in paleolimnology which could influence diatom communities? To this end, I developed diatom-based transfer functions from variables not commonly used in paleolimnology but which inevitably influence diatom assemblages, such as the lake water CO_2 concentration in the epilimnion.

Chapter II-Is the introduction of benthic species necessary for open-water chemical reconstruction in diatom-based transfer functions?

Is the utilization of all diatom taxa (planktonic versus benthic taxa) necessary for the development of reliable and significant predictive models? What other factors may control such performance? To improve the predictive power of diatom-based transfer functions, not just in regard to paleolimnology but to other ecological issues as well, I examined whether certain characteristics of the species assemblages influence the model

performance. First, I tested whether certain types of diatoms were better at predicting lake water conditions than others (planktonic versus benthic taxa). Second, I compared the ability of taxa to bundle information to the models by controlling the number of taxa included. This lead me to examine whether the "predictive" importance of diatom species within the models are a function of their effective number of occurrences or their tolerance or even the number of species included in the models.

Applied approach

The main project was undertaken within the Canadian Sustainable Forest Management-Network of Centres of Excellence (SFM-NCE). The paradigm is summarized as such: sustainable management by simulation of disturbance patterns for the design of new practices in forestry in order to diminish anthropogenic impacts on lacustrine areas. The evaluation of tools that permits to evaluate the impacts of natural disturbances, such as wildfires and effects of silvicultural practices coupled in a global change perspective, give the required knowledge for a better management of aquatic resources. On the applied side of my dissertation, I've considered all the results I found in the fundamental study. My study took place across the Canadian boreal forest (both eastern and western parts) in mixedwood and in coniferous ecodomains. It was carried out in the provinces of Quebec and Alberta. Logging studies were performed in Quebec due to its longer timber harvesting history, but forest fires' impacts on lakes were conducted both in Alberta and in Quebec in order to encompass regions with greatly contrasting limnological characteristics (surficial geology, morphometry, nutrient condition, etc.).

Chapter III- The last 1000 year wildfire and climatic period: effects on diatom changes in Christina Lake (Alberta, Canada)

The impact of forest fires was investigated in a paleolimnological study on Christina Lake, located in a mixedwood sub region of the boreal forest in northern Alberta (Canada). Given the paucity of long-term studies in forested peatland dominated

systems, I used diatoms to reconstruct past chemical conditions in a sediment core of Lake Christina, in the boreal forest where the fire history of the catchment has been well described by Laird and Campbell (2000). My objective was first to examine whether the trends towards greater total diatom abundance and lower species richness during fire events, as described in a similar study in eastern Canada (Enache and Prairie 2000) were also detectable in lake Christina. Second, because charcoal inputs into the lakes can dramatically increase after fire disturbances, I tested whether the ratio of benthic versus planktonic taxa varied, given the very low planktonic tolerance to low light conditions. Finally, I conducted a study to test whether diatom assemblages during the two last centuries have undertaken a substantial shift since the Medieval Warm period (ca. A.D. 800-1250) in Christina Lake.

Chapter IV- Long and short-term trends in diatom-inferred dissolved CO_2 in a small kettle lake from the Abitibi region: impact of forest fires

In this chapter, I reconstructed past CO_2 concentrations in Lake Francis, a small kettle lake typical of the Abitibi Claybelt Region. From this reconstruction and in conjunction with a fire record derived from charcoal stratigraphy (Carcaillet et al. 2001a, b), I examined whether individual forest fires produce a detectable effect of lake CO_2 concentration and whether the temporal trends in CO_2 corresponded to the documented changes in fire frequency. At the same time I tested whether diatom assemblage changes followed the Medieval warm period (MWP) and the little Ice Age (LIA) period, but also if they were able to track the shift in vegetative composition within the catchment.

Chapter V- A 1200 year paleolimnological study in a small kettle lake in the *Picea mariana*-moss domain (Quebec, Canada). Impacts of fires on the biogeochemistry of lakes from diatom remains.

In the coniferous domain of *Picea mariana*-moss forest, the moisture associated with swamp and thick organic layer that may be incompletely removed by fire may prevent less material to be burnt and exported into the drainage basin. Moreover, *Picea mariana*

and *Pinus banksiana* establish rapidly by seed release from serotinous cones, and following fires even-ages stages are often found coupled with the resurgence of understorey vegetation leading to little floristic vegetation. Consequently I tested whether there was a lesser and a shorter impact of forest fires in such coniferous-dominated catchment on the biogeochemistry on Lac à la Pessière compared with two similar paleoecological studies undertaken in the 100 km southern mixedwood forest in Lake Francis (Enache and Prairie 2000; Philibert et al. submitted). I also compared the nature of runoff from the burnt catchment and the lake diatom community-based response that probably could be different between fires occurring on different vegetation types.

Chapter VI- Impact of mid-20th century logging practices on lake-biogeochemistry in Haute Mauricie (Quebec, Canada) as inferred from diatom remains: implications for sustainable management in the boreal forest.

The impact of partial forest cutting (1935-1960) on lake biogeochemistry was examined in three lakes on the Canadian Precambrian Shield in Haute Mauricie in the mixed-wood forest domain (Quebec), where 60-80 % of the catchment area have been progressively cut during the winter over periods ranging from 5 to 10 years. A paleolimnological study was carried out to determine whether the magnitude of the impact of clear cutting on nutrient losses and associated algal biomass increases proposed by Carignan et al. (2000) and Planas et al. (2000) in the same area, were observed in my study lakes, whose catchment was partially but continuously harvested over a few years (5 to 10 years). I used diatom remains to reconstruct changes in environmental variables of limnological interest (pH, TP, TN and DOC) following timber harvesting and compared diatom composition and related reconstructed variables of limnological interest before and after logging events.

The General Conclusion is about the main results I brought throughout my thesis dissertation and the future perspectives.

The General annex is composed of a similar study I collaborated in concern with my

thesis data. In a fundamental perspective of research in paleolimnology, I also participated in the comparison of the predictive power of standard WA-PLS models with new and powerful tools such as Artificial Neural Networks (ANNs) (in Appendix Racca, Philibert and Prairie, 2001).

You can find as well in the Appendix two diatom floras I identified in the two modern sets of calibration in Quebec and in Alberta.

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Chapitre I

Diatom-based transfer functions in western Quebec lakes (Abitibi and Haute Mauricie): the possible role of epilimnetic CO_2 concentration in influencing diatom assemblages

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Résumé

Les sédiments de surface de 76 lacs dans deux régions à l'ouest du Québec (Abitibi et Haute Mauricie) ont été échantillonné afin d'évaluer les relations qui existent entre les diatomées et les variables environnementales. Parce que les deux régions présentent des communautés diatomiques radicalement différentes, nous avons examiné quels facteurs pourraient être responsables des grandes différences rencontrées dans les communautés des deux zones géographiquement proches. Les données chimiques standard des lacs ont montré très peu de différence entre les régions, même si les régimes de lumière dans l'épilimnion étaient plus faibles en Abitibi. Néanmoins pour les mêmes conditions chimiques et lumineuses dans l'épilimnion, il restait encore une nette séparation des diatomées entre les deux régions laissant ainsi penser que d'autres facteurs intervenaient dans la distribution des espèces. Nous avons remarqué que les concentrations de dioxyde de carbone (CO_2) dans les eaux de surface pouvaient expliquer au moins une part de cette discrimination des espèces. Une analyse canonique des correspondances partielle, contrainte à la seule variable de CO_2 en prenant l'alcalinité et le pH comme co-variables, expliquait 12.5 % de la variance des espèces et était significative. Étant donné le manque de relation entre le carbone organique dissous (COD) et le CO_2 et en raison de la super saturation des lacs en CO_2, nous suggérons que les variations de concentrations en CO_2 seraient dues aux eaux souterraines et la possibilité que cette variable puisse influencer les communautés diatomiques pourrait alors permettre dans certains cas la reconstruction des apports des eaux souterraines dans les lacs. Finalement de nouveaux modèles de prédiction ont été établis pour le Québec en employant la méthode de la moyenne pondérée des moindres carrés « WA-PLS » pour inférer le pH, CO_2, phosphore total (PT), l'azote total (NT), et le COD à partir des diatomées préservées à la surface des sédiments en raison de leur intérêt limnologique.

Abstract

Surficial sediments from 76 lakes from two western Quebec regions (Abitibi and Haute Mauricie) were sampled to identify the relationships between diatoms and environmental variables. Because the two regions contained radically different diatom communities, we then investigated which factors may be responsible for the large community discrepancies in the two nearby geographical areas. Standard lake chemistry variables showed little differences between the regions, although epilimnetic light regimes were slightly lower in Abitibi. Nevertheless, lakes of the two regions with similar light regimes and chemistry still showed a clear separation in their diatoms, implying that other important factors are influencing assemblages. We found that the calculated concentration of CO_2 in the open water can explain some of the discrepancy in diatom assemblages. A pCCA constrained to the concentration of CO_2 with alkalinity and pH as co-variables explained 12.5 % of species variance and was significant. Given that the lack of relationship between DOC and CO_2, and because the lakes are heavily supersaturated with CO_2 in the calibration set, lake-to-lake variations in CO_2 concentrations are likely due to groundwater inputs, the possibility that this environmental variable may be influencing diatom communities might allow, in some cases, the reconstruction of historical changes in groundwater inputs to lakes. Finally, new calibration models were built in Québec by using weighted averaging partial least square (WA-PLS) techniques in order to infer pH, CO_2, TP, TN, and DOC from diatom assemblages preserved in the surface sediments because of their limnological interest.

Introduction

Over the last ten years, paleolimnology has seen an extraordinary development of modern calibration sets that are capable of inferring a wide range of environmental variables. These data sets, based on diatoms, chrysophytes, chironomids, cladocera, and other paleo-environmental indicators, now exist for many regions (e.g., Cumming et al. 1992; Birks, 1998; Lotter et al. 1998; Sarmaja-Korjonen and Alhonen, 1999). In the hope of extending previous calibration functions developed from lakes in the Abitibi region of Quebec (Enache and Prairie 2002) to other regions of the Quebec boreal landscape, we have developed a calibration set of 76 lakes in western Quebec combining lakes from the Abitibi and Haute Mauricie regions. These regions are in close proximity (less than 200 km) but are underlaid by very different surface geology and have different glacial histories. The main objective of this paper was to explore the relationship between modern-day diatom assemblages along environmental gradients encompassed by the two regions, and to identify the environmental variables that would best explain the species distribution in our lakes. During the preliminary stages of this investigation, it became clear that the two regions harboured very different diatom communities despite their geographic proximity. First, we examined whether regional variations in chemistry could account for these distinctive communities. In particular, we investigated whether CO_2 concentrations in the open-water may be a contributing factor to this distinction. Reconstructing this variable, which has not yet been used in paleolimnology, may be of great interest in the reconstruction of groundwater inputs to lakes and /or metabolic balance. This does not prohibit the development of general transfer functions combining assemblages from the two regions. In a second step, WA-PLS algorithms were employed to develop transfer functions for pH, CO_2, total phosphorus (TP) total nitrogen (TN), and, dissolved organic carbon (DOC) because of their limnological interest.

Study sites

The calibration set consists of 76 lakes, with 41 from Abitibi and 35 from Réservoir Gouin (Haute Mauricie), as shown in Figure 1.1. All the study lakes are located on the Precambrian Canadian Shield. The Haute Mauricie area lies on glacial till, where surficial deposits are mainly composed of glacio-lacustrine fine grains and tills. In contrast, Abitibi is part of the Clay Belt region of Quebec, which is dominated by clay deposits. Vegetation in both regions is typical of the boreal forest. The Haute-Mauricie and southern part of Abitibi (below 49°N) are dominated by white birch (*Betula papyrifera*), whereas the northern part of Abitibi (above 49°N) is mainly composed of black spruce (*Picea mariana*) forests. In southern Abitibi, balsam fir (*Abies balsamea*), white birch and white spruce are dominant on mesic sites, whereas black spruce, *Thuja occidentalis*, *Larix laricina* associated with *Fraxinus nigra* and *Ulmus americana* are dominant on bogs and hydric sites. Species of poplar (*Populus tremuloides, P. balsamifera*), and white birch are dominant on sites that were affected by forest fires (Bergeron and Dubuc 1989). The northern part of Abitibi is dominated by spruce species (*Picea glauca*, *P. mariana*) and jack pine (*Pinus banksiana*). The Haute Mauricie region is dominated by white birch but also balsam fir, black spruce, and jack pine (*Pinus banksiana*) (Ordre des ingénieurs forestiers du Québec, 1996). Overall, the study lakes from the two regions are fairly shallow (median maximum depth = 10 m), and small (0.01-2.31 km^2), with watershed areas ranging between 0.09 and 19.72 km^2. The water chemistry of the lakes is diverse (Table 1.1). The lakes range from clear to dark, with corresponding DOC concentrations between 1.8 and 18.5 $mg.l^{-1}$ DOC. The lakes are mostly dimictic, except for the very shallow lakes, which do not stratify. In Abitibi, lakes range from oligotrophic to eutrophic (TP = 2.8-52 $\mu g.l^{-1}$), a range that encompasses the entire range of lakes in Haute-Mauricie (TP = 4.9-16.5 $\mu g.l^{-1}$). TN and Chla concentration ranges in Abitibi (TN = 79 to 1489.5 $\mu g.l^{-1}$, Chla = 1.5-245.50 $\mu g.l^{-1}$) encompass those in Haute Mauricie (TN = 138.26-556.18 $\mu g.l^{-1}$, Chla = 1.11-4.82 $\mu g.l^{-1}$). Similarly, the lakes in Haute Mauricie are slightly acidic to circumneutral (pH = 5.6-7.0) whereas lakes in Abitibi span

a pH range between 4.2 and 8. Climate variables (temperature and precipitation) of the two regions are similar due to their close proximity.

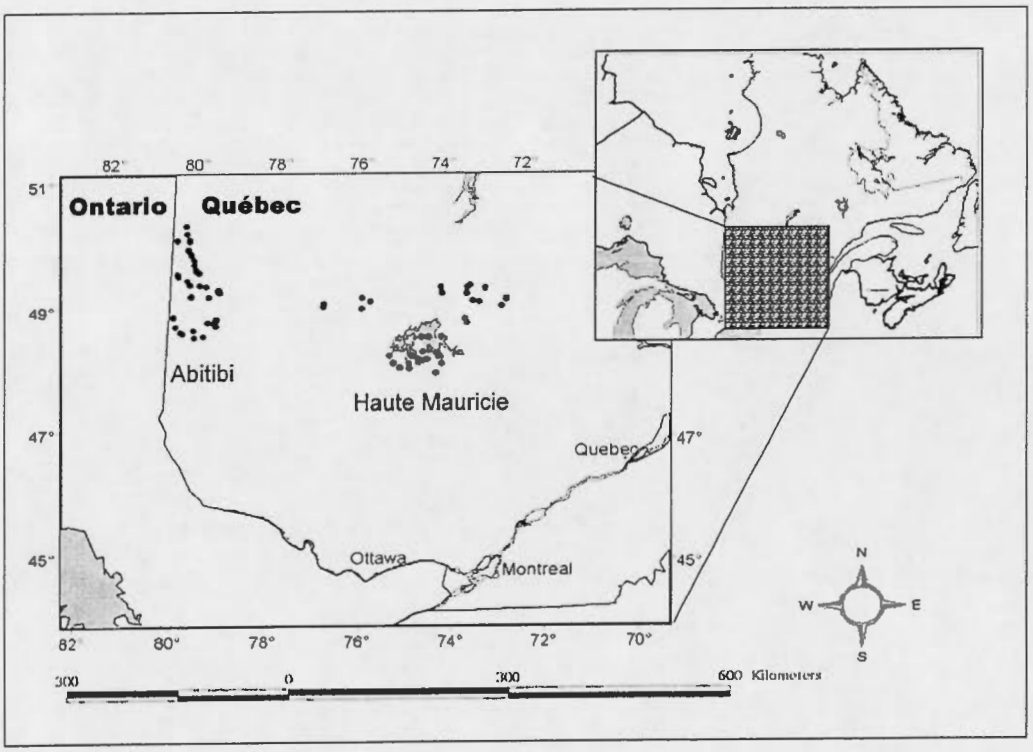

Figure 1.1 Map showing sampling sites. Lakes sampled are presented by solid circles.

Material and methods

Sampling and measurement of environmental variables

Lakes in Haute-Mauricie were sampled three times during the ice-free season (June, mid July and early October) from 1996 and 1997, while the lakes in Abitibi were sampled twice during June-August in 1996 (n = 20) and 1997 (n = 22) (Enache and Prairie 2002). Water samples were taken from the euphotic zone, and kept cold (4°C) for laboratory analysis. Measurements of physical variables and pH were carried out in the field. Integrated surface water samples of the epilimnion were collected in clean polyethylene bottles and immediately transferred to acid-washed and rinsed glass tubes (triplicates) for nutrient analyses. Dissolved organic carbon (DOC) was measured by infrared gas analysis after sample acidification and sparging followed by Pt-catalysed oxidation at 700°C. Samples collected for dissolved species were filtered in the field using 0.45 μm Nalgene membrane syringe filters and sent (within 24-48 hours) to the laboratory of the Université de Montréal (Haute Mauricie samples) and to the Université du Québec à Montréal (Abitibi samples). For both areas, total phosphorus (TP) was measured using the molybdenum-blue method (Stainton et al. 1977), after autoclaving with potassium persulfate; and total nitrogen (TN) after alkaline persulfate digestion and autoclaving (D'Elia et al. 1977). All chemical analyses were performed on an ALPKEM RFA 300 auto-analyser or a Lachat using standard methods. CO_2 concentrations were obtained from pH and alkalinity measurements (Gran titration) following Stumm and Morgan (1981) after correction for ionic strength (Cole et al. 1994).

Sampling and preparation of diatoms

Surface sediment samples (top 1 cm representing a few years) were taken with a gravity corer from the deepest point in the lakes (Glew 1988). Cores were sub-sampled with a vertical extruder in the field. Samples were kept in cool storage and returned to the laboratory for subsequent analyses. Modern diatoms (those recovered from the

surface sediments of the calibration lakes) were processed and counted following standard techniques (Smol 1983; Battarbee 1973, 1986). For each sample, a minimum of 500 diatom valves was counted and identified along random transects at a magnification of 1600X using a Leica DMR microscope. Data taxonomy and nomenclature were primarily based on Krammer and Lange-Bertalot (1986-1991) and Hustedt (1930-1966). This study was done in comparison with a parallel study on the lakes of Abitibi region (Enache and Prairie 2002). The two taxonomists consulted with each other in order to ensure consistent diatom identification.

Data analyses

Multivariate statistical analyses were used as a tool for the interpretation of site data on diatom assemblages and the measured environmental variables (ter Braak 1987). Nineteen variables were measured and integrated in the statistical analyses to explain the diatom species variance (see Table 1.1). Physical properties considered included lake area (LA), drainage area (DA), ratio of drainage area on lake area (DA/LA), ratio of drainage area on volume (DA/VOL), water residence time (Tw), depth (Z), maximal depth (Z max), and Secchi transparency. For light regime, we calculated the average fraction of incident light within the epilimnion (LUM) by integrating the exponential decline to the thermocline depth. For very shallow lakes ($Zmax_{.} < 5$ m), we assumed the epilimnion covered the entire depth. The chemical variables such as dissolved organic carbon (DOC), total phosphorus (TP), total nitrogen (TN), nitrate (NO_3), ammonium (NH_4), pH, alkalinity (ALK), calcium (Ca), magnesium (Mg), and chlorophyll *a* (Chla) were also measured. Similarities between diatom assemblages of the two regions were compared using detrended correspondence analysis (DCA). The DCA was carried out using CANOCO version 3.12 (Jongman et al. 1987; ter Braak 1988a, 1990b). Canonical variate analysis (CVA) was carried out to determine if linear combinations of the physical or chemical properties could discriminate the Abitibi and Haute Mauricie regions. This was done to determine which factors were responsible for the disparities or similarities in diatom assemblages between both regions. The CVA analyses were performed using the

computer program CANOCO version 3.12 (Jongman et al. 1987; ter Braak 1988a, 1990b). Prior to the development of transfer functions, a series of detrended canonical correspondence analyses (DCCA), constrained solely to each environmental variable, were performed to first determine the species gradient lengths with respect to the selected variable, and to determine if unimodal- or linear-based models of reconstruction were most appropriate (Birks 1995). Furthermore, DCCA ordinations were used to establish the significance of selected variables in the explanation of diatoms distributions and therefore to choose the variables that are likely the best predictors of species changes (Birks 1995). This was achieved using the computer program CANOCO version 3.12 (Jongman et al. 1987; ter Braak 1988a, 1990b). Quantitative calibration models, or transfer functions, were developed for the reconstruction of variables from diatom assemblages found in the modern calibration set (76 lakes). The Weighting Average Partial Least Squares (WA-PLS) technique was used because it takes into account both the unimodal response of diatoms along environmental gradients, and the information contained in the residuals, thereby diminishing bias (ter Braak and Juggins 1993). The predictive ability of the calibration models was assessed using the apparent coefficient of determination (r^2) between measured and the diatom-inferred values, and the apparent root mean squared error (RMSE). We also used estimates based on jackknife resampling, $r^2_{jackknife}$ and $RMSE_{jackknife}$, because they represent more realistic measures of the predictive power than the apparent r^2 or RMSE. The analyses were carried out using a SAS/IML implementation of the WA-PLS algorithm (Prairie, unpublished program).

variables		minimum	maximum	mean	median	S.D.	variables		minimum	maximum	mean	median	S.D.
LAT (N)	A	48.27	49.71	48.93	48.90	0.42	DOC ($mg.l^{-1}$)	A	1.75	18.45	9.85	9.21	4.28
	HM	47.87	48.97	48.38	48.34	0.39		HM	2.70	12.80	5.99	5.22	2.42
	C	47.87	49.71	48.69	48.70	0.48		C	1.75	18.45	7.99	6.67	4.00
LON (W)	A	-79.47	-78.64	-79.09	79.16	0.24	TP ($\mu g.l^{-1}$)	A	2.75	52.00	12.88	10.50	9.42
	HM	-76.72	-73.32	-74.77	47.80	0.75		HM	4.85	16.45	5.55	7.68	3.10
	C	-79.47	-73.32	-77.03	78.67	2.25		C	2.75	52.00	10.75	9.00	7.44
ALT (m)	A	280.00	396.00	318.5	320.0	27.29	TN ($\mu g.l^{-1}$)	A	79.00	1489.50	333.1	303.80	238.75
	HM	391.00	558.00	448.5	442.0	36.01		HM	138.26	556.18	250.72	233.88	77.14
	C	280.00	588.00	381.0	373.5	73.99		C	79.00	1489.50	292.00	250.50	184.65
LA (km^2)	A	0.01	1.17	0.17	0.09	0.22	NO3 ($\mu g.l^{-1}$)	A	0.04	35.00	4.64	3.00	6.33
	HM	0.16	2.38	0.50	0.38	0.38		HM	1.03	298.70	23.76	11.20	53.64
	C	0.01	2.31	0.31	0.28	0.33		C	0.04	298.70	13.06	4.96	36.73
DA (km^2)	A	0.09	15.08	2.01	1.06	2.76	NH4 ($\mu g.l^{-1}$)	A	3.50	657.00	31.49	12.50	99.47
	HM	0.44	21.68	3.43	2.54	3.80		HM	3.62	13.36	6.41	5.84	2.38
	C	0.09	19.72	2.54	1.76	3.11		C	3.50	657.00	19.52	8.95	72.79
DA/LA	A	2.81	48.76	15.93	12.00	11.43	pH	A	4.16	8.00	6.20	6.14	0.96
	HM	1.90	42.00	7.39	6.30	6.29		HM	5.64	6.98	6.42	8.45	0.31
	C	2.00	48.76	11.20	8.80	9.82		C	4.16	8.00	6.31	6.40	0.74
DA/VOL	A	0.54	28.56	5.85	4.70	5.27	ALK ($\mu eq.l^{-1}$)	A	0.01	2495.00	331.31	139.00	472.23
(km2/m3 exp-7)	HM	0.24	5.86	1.72	1.29	1.35		HM	15.38	152.35	52.22	44.15	29.58
	C	0.25	28.56	3.84	2.58	4.41		C	0.01	2495.00	196.00	56.20	364.59
Tw (year)	A	0.08	3.62	0.66	0.53	0.60	Chla ($\mu g.l^{-1}$)	A	1.50	245.50	10.67	3.50	37.50
	HM	0.33	5.70	1.63	1.29	1.22		HM	1.11	4.82	2.30	1.89	0.95
	C	0.08	5.58	1.09	0.77	0.98		C	1.11	245.50	6.67	2.50	27.35
Z max (m)	A	1.44	9.01	3.31	6.20	1.69	Ca ($\mu g.l^{-1}$)	A	0.24	16.66	4.09	2.60	4.36
	HM	5.00	34.00	14.06	21.50	6.24		HM	1.00	2.75	1.64	1.48	0.48
	C	1.00	34.00	10.86	10.00	6.89		C	0.24	16.66	2.56	1.64	2.92
Z (m)	A	1.44	9.01	3.31	2.80	1.69	Mg ($\mu g.l^{-1}$)	A	0.19	3.47	0.88	0.54	0.84
	HM	2.10	10.10	4.89	4.60	6.58		HM	0.25	0.87	0.49	0.44	0.16
	C	1.44	10.00	4.02	3.66	1.90		C	0.19	3.47	0.63	0.45	0.55
secchi (m)	A	0.25	6.63	2.11	1.57	1.46	LUM (%)	A	0.09	0.45	0.20	0.17	0.09
	HM	1.40	5.95	3.55	3.80	1.25		HM	0.11	0.45	0.30	0.32	0.08
	C	0.25	6.63	2.85	2.46	1.57		C	0.09	0.45	0.25	0.24	0.09
							CO_2 (μM)	A	12.7	1037	227	149.80	243
								HM	17.95	111.57	39.24	34.16	18.45
								C	12.7	1037.4	137	49.30	199

Table 1.1 Summary of the ranges of environmental variables for both study regions (Abitibi and Haute Mauricie). Abitibi (A), Haute Mauricie (HM), Combined regions (C) abbreviations are explained in the text.

Results

General taxa description

Descriptive details regarding the taxa, with at least 1% abundance in one lake, can be found in Appendix 1. Planktonic taxa were most abundant in 70% of the lakes. Dominant taxa included *Asterionella formosa, Aulacoseira italica* var. *subarctica, Cyclotella bodanica* var. *lemanica, C. stelligera* and *Tabellaria flocculosa.* The most widely represented benthic taxa were *Brachysira brebissonnii, Eunotia bilunaris, E. incisa* and *Frustulia rhomboides.* Hill's N2, an index of evenness which takes into account both the number of occurrences and the relative abundance, gave higher weights to the following taxa: *Cyclotella stelligera, Tabellaria flocculosa, Aulacoseira italica* var. *subarctica, Achnanthes minutissima, Cyclotella bodanica* var. *lemanica, Brachysira brebissonnii* and *Frustulia rhomboides.* However, radical differences in taxa were found between both regions at both the genus and species levels. *Actinella, Cymbella, Cyclostephanos, Diploneis* and *Denticula* were almost solely found in Abitibi. Greater numbers of *Fragilaria* and *Navicula* were also found in Abitibi. Conversely, *Asterionella formosa, Tabellaria binalis* and *T. quadrisepta* were only reported in one lake from Haute-Mauricie. Most species of *Eunotia* were found in Haute Mauricie

Statistical analyses

Similarities and dissimilarities in species assemblages

To explore the similarities or dissimilarities in diatom assemblages between Abitibi and Haute Mauricie, a DCA grouping all taxa (214) was carried out. The percentage of cumulative variance captured by the two first axes was 11% of the species data. The first two axes of the DCA were significant according to Monte Carlo permutation tests (with 199 unrestricted permutations, $p < 0.05$). The DCA showed a distinct and a clear separation of the two study regions in terms of species assemblages (Figure 1.2). Examination of Figure 1.2 also showed that assemblages were more similar in lakes from

the Haute Mauricie area than those in Abitibi, probably due to the greater range in environmental variables in Abitibi as shown in Table 1.1. Key species responsible for the separation shown in the DCA were both planktonic and benthic, suggesting that the two types of habitats are affected. Without mentioning rare species (with low occurrence) or species present at low average relative abundances, several key species in diatom assemblages may be attributed to each region. The key species in Abitibi are *Aulacoseira distans*, *Fragilaria virescens* var. *exigua*, *Frustulia rhomboides* var. *crassinervia*, *Eunotia tenera* and *Tabellaria ventricosa*. In Haute Mauricie, the very common species are *Aulacoseira italica* var. *subarctica*, *Asterionella formosa*, *Cyclotella comensis*, *C.* var. *lemanica*, *Eunotia pectinalis*, and *Tabellaria quadrisepta*. In Abitibi, the majority of environmental variables encompass the entire ranges of those in Haute Mauricie. As a further check, we temporarily reduced our data set to include only lakes that fall within the similar range for pH, TP, TN, DOC, LUM, Zmax, Tw, ALK, Ca, Mg, and DA/VOL. A DCA run on this reduced data set (number of lakes = 10) again showed the same discrepancy in diatom assemblages between the two regions (see Figure 1.3), clearly suggesting that differences in diatoms were due to another factor we had not yet considered.

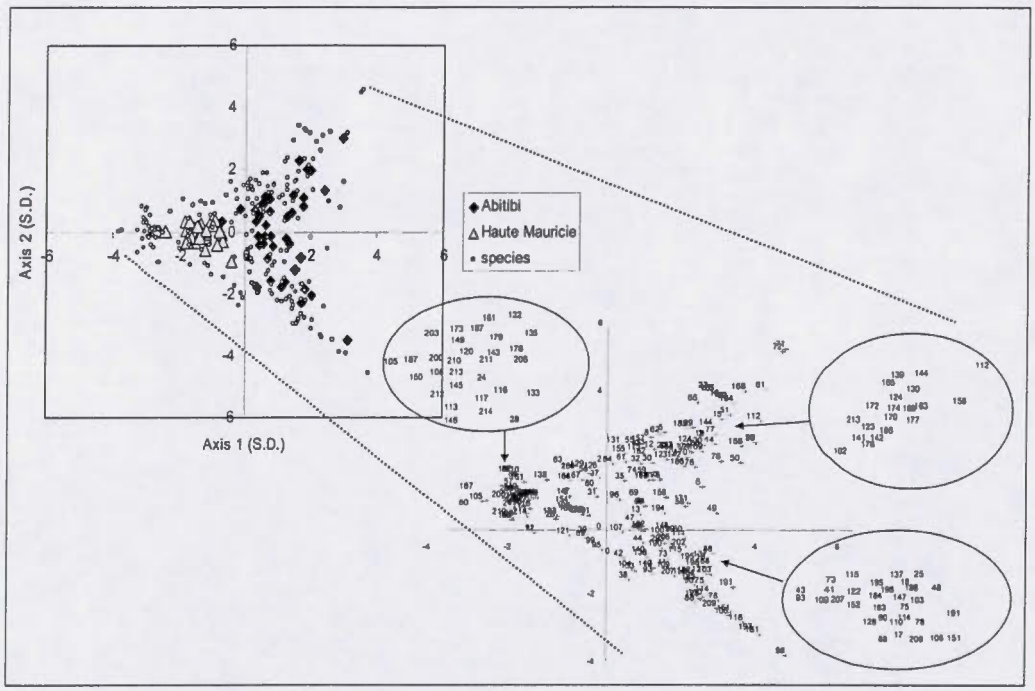

Figure 1.2 Detrended correspondence analysis (DCA) of the 77 lake set.
DCA is a biplot of samples according to their similarities in diatom assemblages. Species numbers listed in Appendix 1.

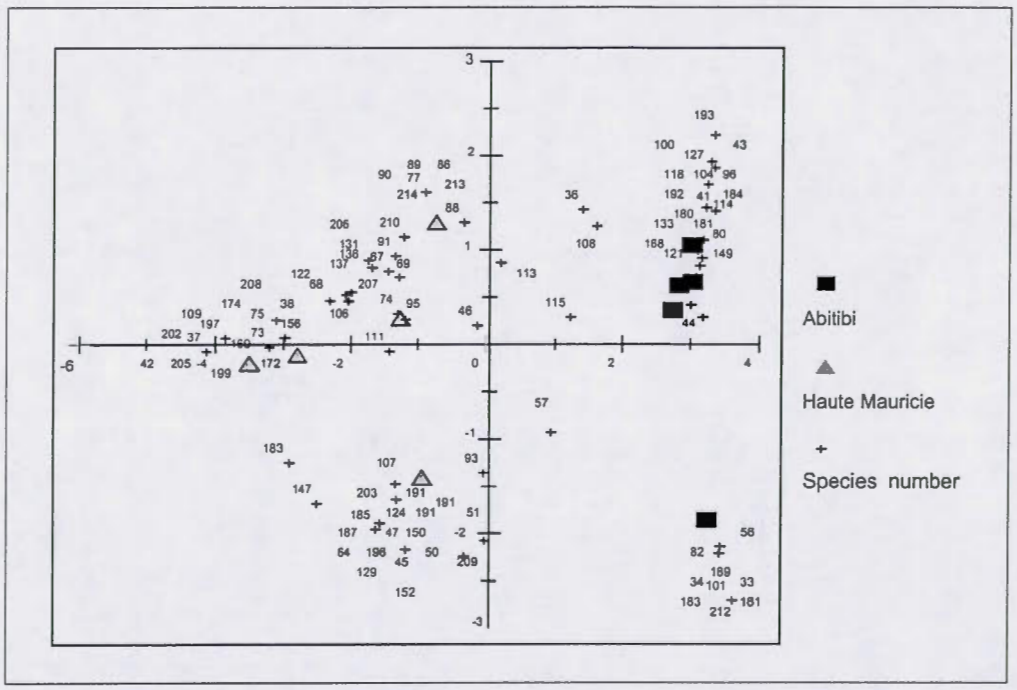

Figure 1.3 Detrended correspondence analysis (DCA) showing biplot of lakes according for their similarities in diatom assemblages.
All lakes used in the DCA have similar limnic properties. We limited the calibration set to a reduced set including only lakes within a defined range of pH, TP, TN, DOC, Zmax, Tw, ALK, Ca, Mg, LUM and DA/VOL found in the Abitibi and in Haute Mauricie regions. Species numbers correspond to Appendix 1.

Although the ranges in both pH and alkalinity of the two regions completely overlap with one another, we were surprised to find that the relationship between the two (log alkalinity versus pH) greatly differed between the regions, with the pH of Abitibi lakes much lower for any given alkalinity (Figure 1.4). Relative to the expected relationship based on the equilibrium chemistry of carbonate-bicarbonate system with the atmosphere, the lakes in Abitibi showed the greatest departure. In this region, alkalinity is essentially carbonate alkalinity and therefore the departure from equilibrium illustrated in Figure 1.4 necessarily imply that the Abitibi lakes are strongly supersaturated with CO_2.

Lakes in equilibrium with the atmosphere should have a dissolved CO_2 concentration in summer around 14-17 μM depending on temperature, ionic strength and elevation. The median dissolved [CO_2] in the Abitibi lakes was 168 μM (range: 13 to 1037 μM), about six times higher than in Haute Mauricie (34 μM). Consequently, we paid more attention to the concentration of free dissolved CO_2 in the open-waters. A CVA was carried out to identify explanatory environmental variables that may account for the disparity in diatom assemblages in the reduced data set (10 lakes). With the exception of pH and DOC, all variables were log transformed to satisfy the assumption of normality prior to the CVA. The environmental variables with high variance inflation factors (VIF) were eliminated to reduce multicollinearity among variables with VIF variates > 10 were excluded (ter Braak 1988a). This CVA was carried out by including [CO_2]. After a forward selection in the CVA, only [CO_2] was retained with a significant t-value. Monte Carlo permutation tests were used to test the significance of the first Axis. The CVA with this single variable captured 51% of the variance in both clusters represented by Abitibi and Haute Mauricie. A CVA on all 76 lakes with CO_2 as the sole variable captured 12.5% of the species variance. CO_2 was able to discriminate between the two regions. In the whole calibration set, when both pH and alkalinity were included as covariables to partial out their influences, the first Axis of the pCCA constrained to CO_2 was still longer significant using Monte Carlo permutation tests (with 199 unrestricted permutations, $P < 0.05$) and explained 12.5% of the species variance. A CCA constrained to CO_2 explained 13.7% of the species variance. Then, WA-PLS CO_2 models were run from our calibration set to test whether we could statistically model the present-day responses of diatom species to dissolved CO_2 concentrations. Useful predictive models were developed (Table 1.2). *Eunotia bilunaris* (89), *E. rhomboidea* (114) and *Pinnularia braunii* (189) are high CO_2 taxa relatively to, for example, *Cymbella cesatii* (71) and *C. delicatula* (72) which are more common in low CO_2 concentration habitats (see Appendix 1).

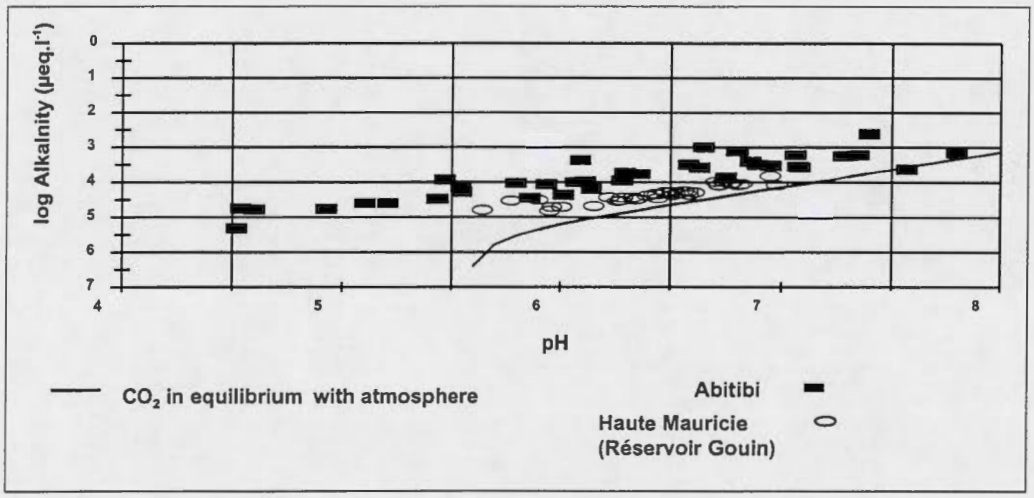

Figure 1.4. Relationships between log alkalinity ($\mu eq l^{-1}$) and pH (units) in both regions. The values in Abitibi are represented by open circles and those in Haute Mauricie by black squares. The curve represents the limit of CO_2 saturation in water depending on the altitude and the temperature. In summer temperatures, the CO_2 concentration in surface freshwaters in equilibrium with the atmosphere is much lower, at around 14-17 µM. All lakes (except Matissar in Abitibi) are supersaturated in CO_2.

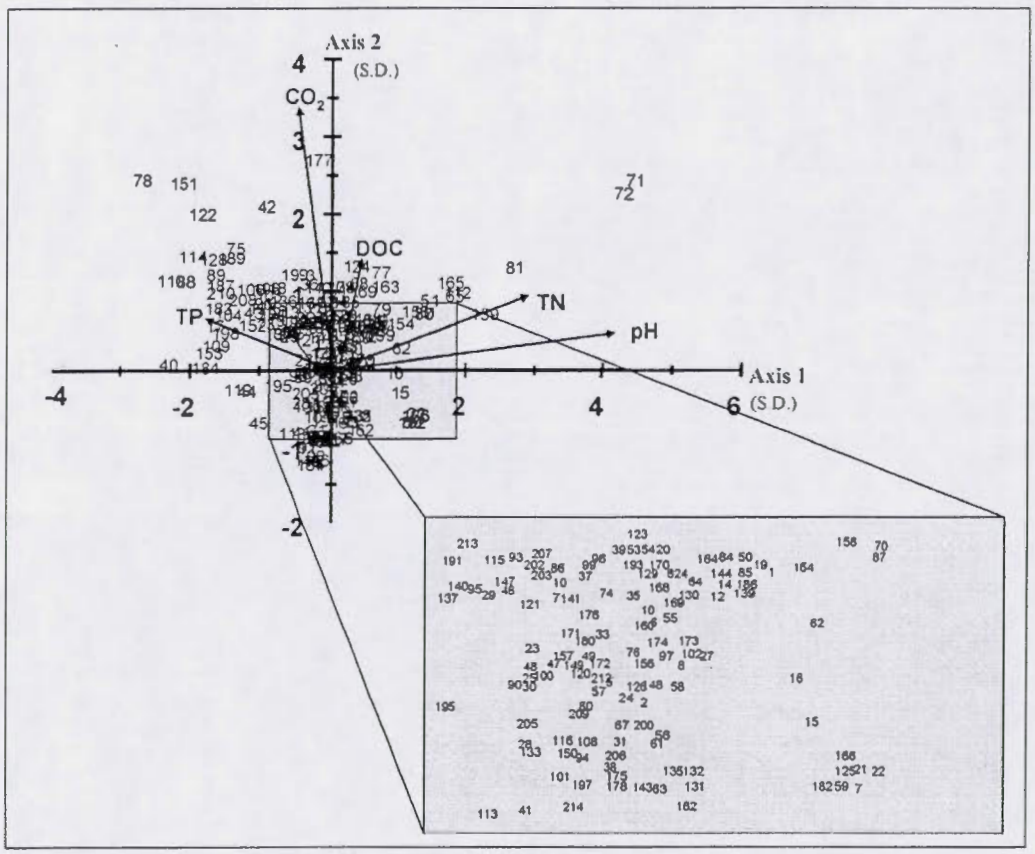

Figure 1.5 Canonical correspondence biplot showing the 5 forward-selected environmental variables.
Variables are represented by arrows as pH, TP, TN, DOC and LUM. Species number listed in Appendix 1.

Species ordination related to variables

Across all sites, a total of 214 diatom taxa occurring at least at 1% abundance in at least one lake and were retained for statistical analyses. The ranges of quantitative variables are summarised in Table 1.1. A CCA was executed on the forward-selected variables and in which we were interested (pH, TP, TN, DOC, and CO_2). Each variable is important to predict quality and dynamics within ecosystems. While TP and TN determine, respectively, the trophic level and the quantity of available nitrogen, pH

values indicate the acidic level in the lake. DOC is of great interest for assessing one potential source of carbon for diatoms, as well as, being an indicator of light penetration influencing the primary production. Finally, CO_2 may be an indicator of the contribution of groundwaters into the lakes. As expected, the mean fraction of incident light in the epilimnion (LUM) was not selected after forward selection in the CCA, due to its strong correlation with DOC in our calibration set. The CCA was able to separate diatom taxa (Figure 1.5) and explained 12.7% of the diatom species variance. *Denticula elegans* (81) and *Cymbella cesatii* and *C. delicatula* (71-72) appear to favour high pH conditions, while *Aulacoseira lacustris* (40), *Frustulia rhomboides* var. *saxonica* (153) and *Neidium iridis* (184) prefer acidic waters. Taxa characteristic of high TP include *Achnanthes flexella* var. *flexella* (7), *Actinella punctata* (17), and *Frustulia rhomboides* var. *saxonica* (153). In contrast, *Cyclotella gamma* (59) and *Navicula diluviana* (166) prefer oligotrophic systems. Taxa plotted in the upper right quadrat have affinities for high concentrations of TN as *Cymbella cesatii* (71) and *Cymbella delicatula* (72), wheras, *Achnanthes biasolettiana* (1), *Aulacoseira perglabra* var. *floriniae* (45), and *Pinnularia mesolepta* (194) are found in low TN conditions. While *Cyclotella stelligera* (68) and *Cymbella microcephala* (77) prefer high DOC and low light conditions at the same time, *Cyclotella ocellata* (63) and *Fragilaria pinnata* sp. (143) favour opposite conditions. We compared our species distribution with those of two recent studies close geographically in Fallu and Pienitz (1999) and in Reavie and Smol (2001). If, generally, the species in common with Reavie and Smol (2001) possess some similar TP optima (mesotrophic systems), they show higher pH and higher TN optima. Even if the DOC range in Fallu and Pienitz is similar to our study (2.3-19.4 $mg.l^{-1}$), no significant correlation was reported between optima for the species in common. We noticed also in this latter study that the study lakes were deeper and show very low alkalinities compared to our present study lakes.

Transfer functions

The WA-PLS models have already been established for the Abitibi region (Enache and Prairie 2002). A series of constrained DCCAs determined that pH, TP, TN, DOC, and CO_2 were significant with Monte Carlo permutation tests (with 199 unrestricted permutations, $P < 0.05$). The first Axis of a DCCA constrained to pH had a gradient length of 3.84 standard deviations (S.D.), indicating that unimodal-based techniques were most appropriate for pH reconstructions. The gradient length of the other variables was also high enough for using unimodal-based techniques (i.e. S.D. > 2). A pCCA constrained on CO_2 with alkalinity and pH as covariable was significant with Monte Carlo permutation tests (with 199 unrestricted permutations, $P < 0.05$). Conversely, a pCCA based on alkalinity with CO_2 and pH was not significant. The pCCA constrained on TP with TN or DOC as covariable was also significant. The same was observed with a pCCA constrained on DOC with TP as covariable. Finally, pH, TP, TN, DOC and CO_2 were considered as potential candidates for predictive models. The WA-PLS model with untransformed species percentage data showed the strongest relationship between diatoms and pH, TP, TN, DOC, and CO_2 reconstructions for any selected variable were all significant and performed well. The regression equations for pH, TP, TN, DOC and CO_2 and prediction errors are summarised in Table 1.2. $r^2_{jackknife}$ in the calibration set are highly influenced by rare species and by the disparity of diatom assemblages between both regions. The apparent r^2 for pH and CO_2 respectively reached 0.91($r^2_{jackknife}$ = 0.69) and 0.93 ($r^2_{jackknife}$ = 0.58). The WA-PLS CO_2 calibration models are shown in Figure 1.6. For TP and DOC, we obtained, respectively, 0.89 and 0.64 ($r^2_{jackknife}$ = 0.51 and 0.34). The relation between inferred and observed values was also strong and significant for TN (r^2 = 0.89). There was no systematic bias in the residual plots for any variable.

WA-PLS TP	Abitibi set (n=41)	Haute Mauricie set (n=35)	calibration set (n=76)
number of WA-PLS components for apparent	3	2	2
total explained variance %	78.02	88.22	86.50
apparent r^2	0.93	0.65	0.89
r^2 jack	0.17	0.30	0.51
apparent RMSE ($\mu g.l^{-1}$)	1.78	1.83	1.53
RMSE jack	6.26	2.60	3.20
number of samples used	38	35	72
WA-PLS pH	**Abitibi set (n=41)**	**Haute Mauricie set (n=35)**	**calibration set (n=76)**
number of WA-PLS components for apparent	3	2	3
total explained variance %	83.85	64.67	86.13
apparent r^2	0.94	0.63	0.91
r^2 jack	0.75	0.23	0.69
apparent RMSE (unity pH)	0.25	0.19	0.23
RMSE jack	0.48	0.28	0.42
number of samples used	41	35	76
WA-PLS TN	**Abitibi set (n=41)**	**Haute Mauricie set (n=35)**	**calibration set (n=76)**
number of WA-PLS components for apparent	4	2	2
total explained variance %	68.35	82.06	73.00
apparent r^2	0.93	0.74	0.89
r^2 jack	0.21	0.10	0.36
apparent RMSE ($\mu g.l^{-1}$)	116.05	41.94	59.06
RMSE jack	234.91	78.36	96.59
number of samples used	34	35	69
WA-PLS DOC	**Abitibi set (n=41)**	**Haute Mauricie set (n=35)**	**calibration set (n=76)**
number of WA-PLS components for apparent	2	1	2
total explained variance %	82.07	86.08	86.01
apparent r^2	0.63	0.70	0.64
r^2 jack	0.17	0.39	0.34
apparent RMSE ($mg.l^{-1}$)	2.47	2.39	2.31
RMSE jack	3.77	2.46	3.17
number of samples used	41	35	76
WA-PLS CO_2	**Abitibi set (n=41)**	**Haute Mauricie set (n=35)**	**calibration set (n=76)**
number of WA-PLS components for apparent	3	3	3
total explained variance %	83.47	90.94	87.79
apparent r^2	0.87	0.67	0.93
r^2 jack	0.26	0.10	0.58
apparent RMSE	86.90	10.00	44.00
RMSE jack	212.00	60.00	62.67
number of samples used	39	35	71

Table 1.2: Results of the WA–PLS for the calibration sets.

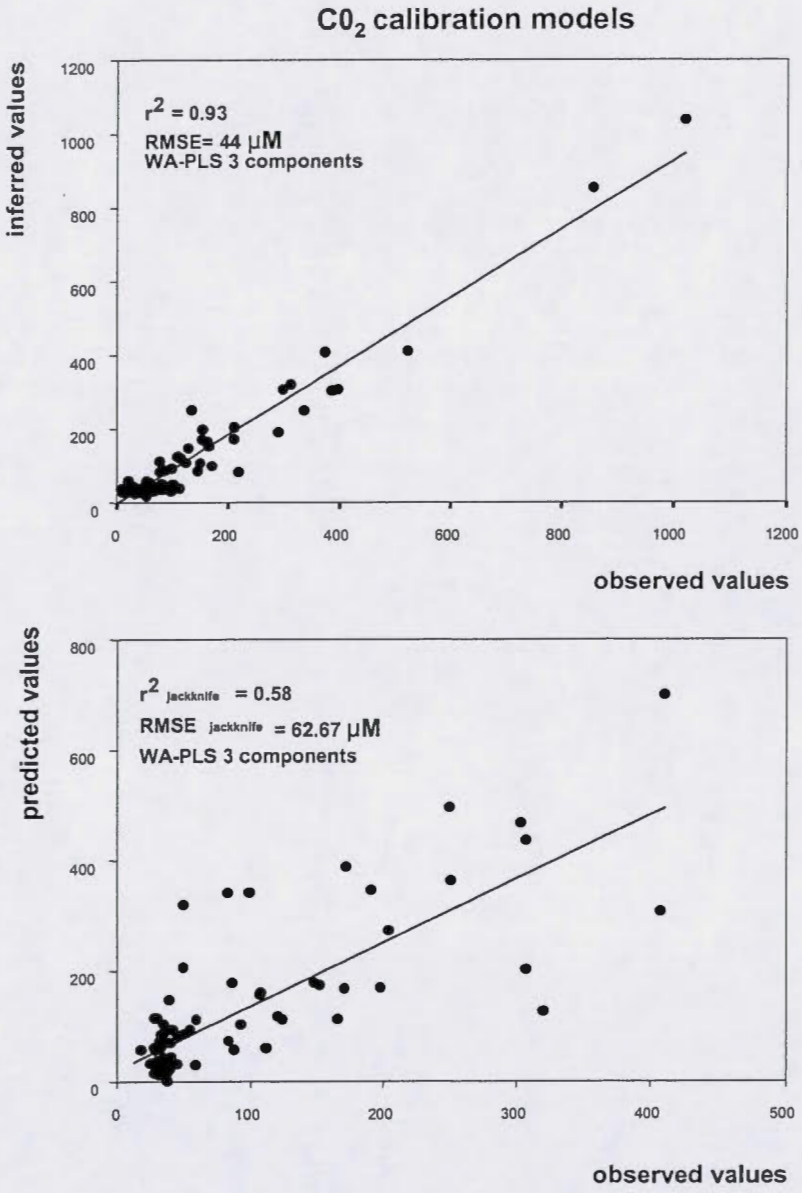

Figure 1.6 Predictive models based on combined data from Abitibi + Haute Mauricie. Plots of inferred and predicted values versus observed values of CO_2 concentrations based on WA-PLS models. The $r^2_{jackknife}$ are highly influenced by the numerous rare taxa (more than 60 % in the calibration set).

Discussion

Regional differences: the importance of CO_2

Our results suggest that when one examines only the standard physical and chemical limnological properties, the lakes of the two regions are quite similar. Yet their diatom assemblages are almost totally distinct, and none of the subtle limnological differences in the classical suite of chemical variables can satisfactorily explain the diatom discrepancies. Even in our restricted data set focussing on lakes of the two regions covering very narrow and similar chemical ranges, the regional diatom separation was clear without any overlap. The clear discrepancy in diatom assemblages also distinguishes planktonic diatoms that inhabit the open water area where similar chemical ranges were observed in the two regions. It is well known that pH, TP TN, DOC and light availability influence diatom assemblages. However, our results suggest that other factors, not previously considered in paleolimnological studies to our knowledge, regulate diatom distribution in these freshwaters, and that the CO_2 concentration, may be a prime candidate. However, because of the chemical relationships between pH, alkalinity and CO_2, it can also be argued that the CO_2 differences are alkalinity differences for a given pH. We suggest here that there is ample evidence in the literature to suggest that CO_2 may directly affect the ability of diatom species to successfully compete in their environment and that diatom also may be physiologically correlated with the CO_2 concentrations (Reinfelder et al. 2000, Gervais and Riebesel 2001, Morel et al. 2002). Firstly, unlike pH and CO_2, alkalinity is a capacity factor (*sensu* Stumm and Morgan 1981) and does not express a concentration. Biologically, it is much easier to demosntrate that diatoms will be influenced directly by a concentration rather than a capacity factor. Secondly, not all algal groups and species are able to utilise bicarbonate as a source of inorganic carbon for photosynthesis. Even for those groups which can, with the possible exception of species adapted to alkaline waters (in particular cyanophytes), CO_2 is generally the preferred substratum when available (Kirk 1994). Thirdly, within the diatoms, the ability to use HCO_3^- also varies widely among species. For example,

Fragilaria crotonensis can effectively use HCO_3^- but *Aulacoseira italica* cannot (Kirk 1994). Fourthly, algal species differ widely in their affinity for CO_2. In the few freshwater species where such studies have been conducted, CO_2 uptake kinetics vary with $[CO_2]$ following a Michaelis-Menten curve, with K_m values ranging between 60 and 140 μM (in Kirk 1994). At summer temperatures, the CO_2 concentration is much lower in surface freshwaters in equilibrium with the atmosphere, at around 14-17 μM. It is therefore not surprising that the much higher concentrations of CO_2 found in Abitibi lakes would favour diatom species with different CO_2 affinities (see Appendix 1) than those found in Haute Mauricie lakes.

Our data are not adequate to identify precisely the sources of the unusually high CO_2 concentrations in the Abitibi lakes, but some hypotheses are more likely than others. For example, even a strongly heterotrophic epilimnetic metabolism cannot realistically generate such supersaturation (Prairie et al. 2002). Even if the epilimnetic oxygen was entirely consumed and converted to CO_2, the maximum CO_2 concentration would be about 280 μM. Several lakes exceed this concentration. In addition, we found that both oxygen and CO_2 were supersaturated in the epilimnion in many lakes. Thus, among lakes, differences in CO_2 are most likely due to variations in the groundwater contribution to the hydrological budgets of individual lakes. The Abitibi region being within the Clay Belt, the surface geology of the area is highly heterogeneous and prone to groundwater infiltration. If it can be shown that, regionally, the CO_2 concentration of groundwater is reasonably homogenous, this opens the possibility of using diatom, as a proxy for groundwater flow into lakes, an important characteristic of lakes that has proved difficult to reconstruct. Photolysis of dissolved organic matter directly to CO_2 is also a possible pathway for CO_2 supersaturation, particularly in acidic conditions (Gennings et al. 2001). However, the lack of correlation between DOC and CO_2, and the magnitude of the supersaturation render this mechanism less plausible. In our view, the most likely explanation involves the infiltration of groundwater heavily laced with CO_2. Even a relatively small contribution of groundwater to the hydrological budget is sufficient to generate vast differences in lakewater CO_2 concentrations.

Although we believe CO_2 is probably the predominant factor in explaining the differences in diatoms between our two study regions, we cannot completely rule out other potentially modulating factors. An alternative explanation may be historical. Our two regions differ markedly in their glacial history. All of our lakes in the Abitibi region are located within the confines of former proglacial Lake Ojibway. Deglaciation of the submerged Abitibi area ended with the drainage of Lake Ojibway into the Tyrell Sea at about 8,470 KA B.P. (Veillette 1994; Prévost et al. 1995; Baber et al. 1999). The Abitibi region lies on the Clay Belt area of Quebec with a substratum composed mainly of (glacio) lacustrine fine grains, silts and clay, whereas the Haute-Mauricie area lies on glacial till. None of the Haute-Mauricie lakes were part of Lake Ojibway. Given the ease with which diatoms can be transported and therefore colonize other areas, diatoms are not physically isolated between the two areas of interest. It is conceivable that the assemblages may have remained clearly distinct due to the different type of substratum developed after the drainage of Lake Ojibway and created different micro-habitats. The type of substrata (e.g. presence of macrophytes, stones, sand) are known to strongly affect the diversity of benthic algae. Unfortunately we do not have sufficient information on the substrata and lake vegetation to substantiate this hypothesis. However, this cannot explain the discrepancy observed in the planktonic species of the two regions, as noted in the results.

Inference models in our combined 76 calibration lakes in Quebec performed well with pH, CO_2, TP, DOC, and TN (Table 1.2), as well as or even better than either regional model. Compared to other published models in the literature, the goodness-of-fit (r^2) of the model was strongest for pH and was comparable to that found in Northern Europe (Birks et al. 1990) and in the Adirondacks (Dixit et al. 1993). Similarly, the $r^2_{apparent}$ obtained for DOC was similar to the Yellowknife area, North-west Territories (Pienitz and Smol 1993). The $r^2_{apparent}$ of our combined TP model was comparable to those in Southeast England (Bennion, 1994) or British Columbia (Reavie et al. 1995). The $RMSE_{jackknife}$ for TN, and DOC were relatively large (Table 1.2), which, we suggest, may be due to the large number of rare species and to the variety of diatom assemblages

observed between the two Abitibi and Haute Mauricie regions. We obtained similar r^2 and RMSE in WA-PLS TN and DOC models by jackknife procedures than in Reavie and Smol (2001), a region relatively close geographically to our calibration set.

Conclusions

Differences in CO_2 concentrations likely explain some of the differences in diatom assemblages recorded between regions. We suggest that dissolved concentrations of CO_2 in open waters may be a useful as a proxy for groundwater inputs and, given their influence on diatom assemblages, they may potentially be reconstructed. Environmental variables associated with nutrient concentrations, pH and incident light in the epilimnion explained significant portions of variation in the diatom flora from Abitibi and Haute Mauricie. Inference models performed well for pH, CO_2, TP, TN, and DOC using WA-PLS methods. These transfer functions should assist future paleolimnological reconstructions of past disturbances by providing a wider range of application and more diverse analogues.

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Chapitre II

Is the introduction of benthic species necessary for open-water chemical reconstruction in diatom-based transfer functions?

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Résumé

Même si la quasi-totalité des modèles en paléolimnologie utilise à la fois les espèces planctoniques et benthiques pour prédire les conditions physico-chimiques en eaux libres, on pourrait se demander si en effet toutes les espèces sont bien utiles. Afin de pousser d'avantage cette réflexion, nous avons travaillé sur un ensemble de calibration constitué de 75 lacs au Québec (Canada). Tout d'abord nous avons évalué si lors de l'omission des taxons benthiques la performance des modèles était affectée. Comme les taxons benthiques sont connus pour nicher sous des conditions chimiques différentes de celles de leur analogues planctoniques, nous avions la présomption que les taxons benthiques pourraient introduire du bruit de fond dans les modèles. À notre grande surprise, les meilleures prédictions pour le pH, le phosphore total (PT), l'azote total (NT) ou encore le carbone organiques dissous ont été obtenues sur des modèles basés uniquement des espèces benthiques. Même en faisant varier la profondeur des lacs nous avons obtenu les mêmes résultats. Si le nombre d'occurrences effective (N2) ou encore la tolérance des espèces influençaient la stabilité de la racine de l'erreur quadratique (en jackknife), le nombre d'espèces inclues dans le modèle était indéniablement le facteur clé qui était responsable quant à la faiblesse des modèles basés uniquement sur les taxons planctoniques. En effet, pour le même nombre d'espèces inclus dans nos modèles, les espèces planctoniques offrent un potentiel de prédiction supérieur à celui des espèces benthiques.

Abstract

Despite the overwhelming tendency in paleolimnology to use both planktonic and benthic diatoms when inferring open-water chemical conditions, it remains questionable whether all taxa are appropriate and necessary to construct useful inference models. We examined this question using a 75-lake training set from Quebec (Canada) to assess whether model performance is affected through the deletion of benthic species. Because benthic species are known to experience very different chemical conditions than their planktonic counterparts, we hypothesized that they would introduce undesirable noise in the calibration. Surprisingly, such important variables as pH, total phosphorus (TP), total nitrogen (TN) and dissolved organic carbon (DOC) were well predicted from Weigthed Averaging -Partial Least Square (WA-PLS) models based solely on benthic species. Similar results were obtained regardless of the depth of the lakes. Although the effective number of occurrences (N2) and the tolerance of species influenced the stability of the model residual error (jackknife), the number of species was the major factor responsible for the weaker inference models when based on planktonic diatoms alone. Indeed, when controlled for the number of species in WA-PLS models, individual planktonic diatom species showed superior predictive power than individual benthic species in inferring open-water chemical conditions.

Introduction

Most recent methodological advances in paleolimnology have focused on methodology for sample collection (Renberg 1981; Glew 1988), chronological techniques (MacDonald et al. 1991), and in particular statistical modelling (ter Braak and van Dam 1989; Birks et al. 1990; ter Braak and Juggings 1993). While these have undoubtedly led to significantly better paleoreconstruction models, it is surprising that few studies have examined some of the more fundamental underpinnings of the paleolimnological approach. For example, accurate estimates of past environmental conditions are based on biological assemblages and assume that we can statistically model the present-day responses of any species in relation to open-water conditions. While this assumption is probably correct for many organisms, it is likely inappropriate for organisms adapted to low-light conditions or to other microhabitats (i.e., inhabiting the hypolimnion or near the sediment-water interface). Because these organisms are essentially sessile, they experience a different range of light intensities depending on the depth and the substratum they are attached to (Vadeboncoeur and Lodge 2000). Moreover, the chemistry of these environments can be markedly different from that of the mixed layer (Wetzel 1983; Hansson 1992; Blumenshine et al. 1997) and there is little evidence of a good correlation between the chemical conditions of these two environments. This problem is particularly acute with paleolimnological calibrations based on diatoms, since in many environments, benthic diatoms often dominate the assemblages (Dixit et al. 1999; Cameron et al. 1999; Fallu and Pienitz 1999). Nevertheless, the great majority of diatom-based transfer functions are based on complete diatom assemblages (pelagic, littoral or benthic species), even if the stated purpose is to predict open-water chemical conditions.

Here, we hypothesize that benthic diatoms are likely to introduce noise in predictive models, because of the disparity of nutrient pools (Blumenshine et al. 1997), coupled with the higher degree of variability in the physical and chemical conditions, under which benthic algae grow (Wetzel 1983; Burkholder and Wetzel 1990). For example, the nature

and distribution of the substratum with respect to light and depth affect the response of benthic algae to changes in water-column nutrients (Vadeboncoeur and Lodge 2000). In addition, fluxes from the sediment can greatly enhance their nutrient supply (Hansson 1992; Scheffer 1998; Siver 1999). Some authors have already argued that it would be more appropriate to base predictive models solely on planktonic species that inhabit the open-water habitat (Bennion 1994; Siver 1999). In particular, Siver (1999) established outstanding models from Connecticut lakes (U.S.A.) solely based on planktonic diatoms for pH, total nitrogen (TN), and specific conductivity. Whether this high performance from using planktonic diatoms alone is a general phenomenon has, however, not been widely tested.

Our main objective in this study was to assess whether the performance of diatom-based inference models can be improved through the omission of benthic species. First, we tested whether calibration models based solely on planktonic diatoms were able to produce robust and reliable prediction of selected environmental variables in the training set. Second, we compared the predictive power of models developed on only planktonic, only benthic species, or by all species combined. Because the relative abundance of planktonic and benthic species is itself a function of lake characteristics, such as lake depth and light penetration, we further examined our hypothesis in shallow and deep lakes separately. In deep lakes (Zmax > 10 m) which stratify during summer, and where planktonic comprise a higher relative abundance than benthic species (a mean of 74%), we expect planktonic diatoms to be superior predictors of environmental variables. In contrast, in shallow lakes (Zmax < 10 m), we expect benthic taxa to have better predictive power.

In addition to habitat type and depth, we further examined whether other potentially confounding characteristics of the species assemblages could influence model performance. Throughout our analyses, we therefore took into account how model performance varied with the number of taxa included in the model, the effective number of occurrence (N2) and the tolerance of each species.

Study sites

Our calibration set consists of 75 lakes, with 40 from Abitibi and 35 from Réservoir Gouin (Haute Mauricie) (Figure 2.1).

Overall, the study lakes from the two regions are fairly shallow (median maximum depth = 10 m) and small (0.01-2.31 km^2), with watershed areas ranging between 0.09 km^2 and 19.72 km^2. The water chemistry of the lakes is diverse (Table 2.1). The lakes range from clear to dark, with corresponding dissolved organic carbon (DOC) concentrations between 1.8 $mg.l^{-1}$and 18.5 $mg.l^{-1}$ DOC. The lakes are mostly dimictic, except for the very shallow lakes, which do not stratify. In Abitibi, lakes range from oligotrophic to eutrophic (2.8-52 $\mu g.l^{-1}$ total phosphorus), a range that encompasses the entire range of lakes from the Haute-Mauricie (4.9-16.5 $\mu g.lL^{-1}$). Similarly, the lakes in Haute Mauricie are slightly acidic to circumneutral (pH = 5.6-7.0), whereas lakes in Abitibi span a wider pH range between (4.2 and 8). Climate variables (temperature and precipitation) of the two regions are similar due to their close proximity (for more details see chapter I- Philibert and Prairie 2002a).

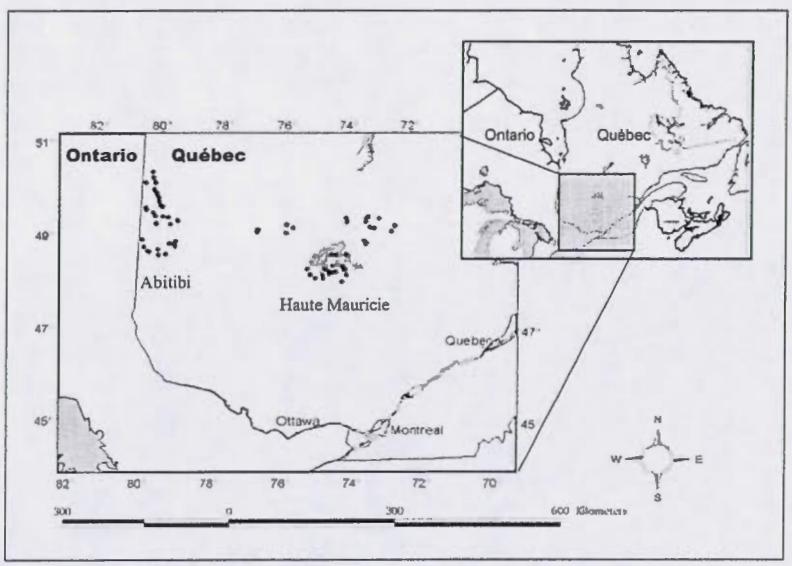

Figure 2.1 Map showing sampling sites in Québec, Canada.
Lakes sampled are presented by solid circles.

variables	minimum	maximum	mean	median	S.D.	variables	minimum	maximum	mean	median	S.D.
LAT (N)	47.80	49.70	48.68	48.79	0.48	DOC ($mg.l^{-1}$)	1.75	16.72	7.98	6.70	3.89
LON (W)	-73.32	-79.47	-77.13	-78.68	2.23	TP ($\mu g.l^{-1}$)	2.75	30.50	10.28	9.00	5.89
ALT (m)	280.00	558.00	377.0	366.0	71.41	TN ($\mu g.l^{-1}$)	79.00	1489.50	249.2	286.31	20.80
LA (km^2)	0.01	2.38	0.32	0.28	0.34	NO_3^{2-} ($\mu g.l^{-1}$)	0.45	146.00	9.70	4.89	17.95
DA (km^2)	0.09	21.68	2.64	1.75	3.33	NH_4 ($\mu g.l^{-1}$)	3.50	657.00	20.31	8.84	75.13
DA/LA	1.90	48.76	11.64	8.79	10.22	pH	4.16	8.00	6.30	6.39	0.76
DA/VOL	0.24	28.56	3.84	2.58	4.38	Alkalinity ($\mu eq.l^{-1}$)	4.30	2495.00	191.93	57.30	362.00
Tw (year)	0.08	5.70	1.11	0.77	1.04	Chla ($\mu g.l^{-1}$)	1.10	32.90	3.71	2.50	4.23
Z max (m)	1.00	34.00	10.69	10.00	6.75	Ca^{2+} ($mg.l^{-1}$)	0.24	16.66	2.57	1.63	2.94
Z (m)	1.44	10.10	4.03	3.66	1.96	Mg ($mg.l^{-1}$)	0.18	3.46	0.62	0.44	0.55
secchi (m)	0.25	6.62	2.78	2.43	1.54	LUM (%)	0.10	0.45	0.25	0.23	0.09

Table 2.1: Summary of the ranges of environmental variables for both study regions (Abitibi and Haute Mauricie).
SD = standard deviation. The variables we measured were the latitude (LAT), longitude (LON), altitude (ALT), lake area (LA), drainage area (DA), ratio DA/LA, volume (VOL), ratio DA/VOL, residence time (Tw), maximal depth (Zmax), mean depth (Z), secchi depth (secchi), dissolved organic carbon (DOC), total phosphorus (TP), total nitrognen (TN), nitrates (NO_3^{2-}), ammonium (NH_4), pH, Alkalinity, Chlorophyll a (Chla), calcium (Ca^{2+}), magnesium (Mg^{2+}) and the fraction of incident light (LUM).

The sampling and the measurement of environmental variables as well as the counting of diatoms followed standard methods. The taxonomy and nomenclature was primarily based on Hustedt (1930-1966); Krammer and Lange-Bertalot (1986-1991). The distinction between planktonic and benthic taxa in our data set was, at times, a difficult and somewhat arbitrary task. We based our classification on what is generally

accepted in the literature. Yet, we fully acknowledge that some "ambiguous" algae exist, (such as *Aulacoseira subarctica*, *Asterionella formosa*, and *Tabellaria flocculosa*), i.e. those that may have been collected in pelagic zones in one study, and referred to as benthic in other areas. On this basis, a maximum of about 7% of the species could be classified as ambiguous and, in these cases, we followed the recommendations of algal taxonomists, including one working on live diatoms from the Haute Mauricie region. Appendix 2 reports the flora description and the "pelagic" or "benthic" appellation attributed to species used in this study. A total number of 214 diatom species were identified, of which 47 were classified as planktonic and 167 as benthic (see Appendix 2).

Material and Methods

Statistical analyses

The training set consisted of a total 214 diatom taxa collected from 75 lakes for which we measured 18 environmental variables (Table 2.1, see for more details the chapter I-Philibert and Prairie 2002a). To test whether the three groups of taxa (planktonic, benthic and combined taxa) conserved the same predictive potential according the maximal depth in lakes, we divided our calibration set of 75 lakes in two classes of shallow and deep lakes. Because the maximum depth in the calibration set ranged from 1 to 34 meters, we chose the depth of 10 meters as a limit between shallow and deep basins. Thirty-five lakes were classified as shallow and 40 as deep lakes.

As Wilson et al. (1996) noted, most calibration data sets published to date have chosen their criteria for species deletion according a minimal percentage of abundance and occurrence in lakes: e.g. 1% abundance in at least one lake (Fritz et al. 1993), 2% in at least one lake (Fritz et al. 1991), or 1% in at least three lakes (Wilson et al. 1996). Because our hypotheses concern the effect of both the number of species and the effective number of occurrence (N2) upon the predictive ability of predictive models, we

used the most inclusive criterion, i.e. all taxa with at least 1% abundance in at least one lake.

Multivariate statistical techniques were used to explore the relationships between environmental variables and diatom taxa and to identify the variables most likely to produce the most reliable inference models. The environmental variables were log-transformed because of their uneveness distribution. A canonical correspondence analysis (CCA) with forward-selection was carried out to select the environmental variables retained for inference models using CANOCO version 4.0 for Windows (ter Braak and Šmilauer 1998). Among the forward-selected variables we were interested in were pH, TP, TN, DOC. Prior to the development of transfer functions, a series of detrended canonical correspondence analyses (DCCA) constrained solely to each environmental variable we were interested in (pH, TP, TN, DOC), were used to establish the significance of selected variables in the explanation of diatom distributions (ter Braak and Prentice 1988; Birks 1995). Furthermore, this series of DCCA were also performed to determine first the species gradient lengths with respect to the selected variable, and to determine whether unimodal- or linear-based models of reconstruction were most appropriate (Birks 1995; 1998). For each environmental variable retained, a DCCA was done with detrending-by-segments, non-linear rescaling in order to estimate the lengths of compositional gradients. This was achieved using the computer program CANOCO version 4.0 for Windows (ter Braak and Šmilauer 1998). Also, a partial canonical correspondence analysis (pCCA) constrained on each variable with or without co-variable was carried out to validate the independent information carried by the individual variables.

Several calibration models that assume a unimodal response between taxa and environmental variables were tested, such as simple weighted averaging (WA) or inverse deshrinking WA, with or without tolerance downweighting of each taxon (Birks et al. 1990). Weighted averaging partial least squares (WA-PLS) using one or several components were also developed. Linear relationships between organisms and their environment were tested from partial least square calibration models (PLS). On the basis

of various simulations and comparisons, the above models were compared in order to assess which one performed the best for each variable. All unimodal models mentioned above, and the linear PLS models were calculated using the computer program Calibrate (WACALIB version 3.3) (Line et al. 1994). In all cases, DCCA models included species gradients with lengths superior to 2 standard deviations (S.D.). Because WA-PLS techniques offered best predictions regardless of the variable, they were used throughout for testing our hypotheses.

We concentrated on statistical requirements for robust models, such as the lowest root mean square error (RMSE). As noted in Birks (1998) model performance statistics such as RMSE are not dependent on the range of the observed environmental gradient, unlike the coefficient of determination (r^2) that measures the strength of the relationship between observed and predicted values (Birks 1998). Apparent RMSE was utilized when testing the effect of lake depth because the combination of only 47 taxa in smaller subsets of lakes (shallow and deep) rendered jackknife procedures highly unstable.

When we performed tests to control for the influence of the total number of species, the tolerance of species, or the effective number of occurrences or Hill's N2 (Hill 1973), we focused our analyses on pH as the main environmental variable. Because of the large and more even pH span between 4 and 8.5, we were able to use jackknife measures of fit and precision and compared our results with other similar studies (Birks 1994; Wilson et al. 1996). All tests performed to assess which factor most influenced diatom distribution and model performance were done using a SAS/IML implementation of the WA-PLS algorithm (Prairie, unpublished program). The WA species tolerance was calculated following weighted averaging. The N2 can be conceived of as the effective number of occurrences of each species. It includes both the occurrences of species and the relative abundances in all lakes within the training set (Hill 1973). N2 is the inverse of the Simpson index.

Results

General relationships

Among the CCA forward-selected variables were pH, total phosphorus (TP), total nitrogen (TN) and dissolved organic carbon (DOC). After a series of constrained DCCAs, the variables pH, TP, TN, DOC were selected as significant environmental variables ($p < 0.05$) that were likely the best predictors of species change. This was done for the three taxa groupings (planktonic, benthic or all species) and for classes of lake depth (shallow and deep, and the whole set of 75 lakes).

Planktonic, benthic or both?

For all environmental variables retained, we were able to develop significant predictive WA-PLS models (3 components) using only planktonic, only benthic or by combining all diatoms (Table 2.2). However, their predictive power differed greatly. Surprisingly, using only planktonic diatoms systematically produced the worst models with RMSE significantly larger than those of either only benthic or all taxa models (F-test on the ratio of the residual variances, $p < 0.05$). The best models were invariably produced when all taxa were included, although their predictive power was statistically indistinguishable from models based on benthic species only (T-test, $p < 0.05$). This same trend was observed for all four environmental variables (pH, TP, TN, and DOC). Independently of the species grouping included in WA-PLS models, pH was the best-predicted environmental variable.

	performance	PH (units)	TP ($\mu g.l^{-1}$)	TN ($\mu g.l^{-1}$)	DOC ($mg.l^{-1}$)
training set n = 75					
planktonic	r^2	0.66*	0.65*	0.82	0.64*
	RMSE	0.44*	3.74*	77.43*	2.32*
benthic	r^2	0.92	0.82	0.88	0.86
	RMSE	0.21	2.51	61.81	1.45
all taxa	r^2	0.94	0.92	0.93	0.89
	RMSE	0.18	1.65	49.38	1.28
deep lakes n = 42					
planktonic	r^2	0.89	0.48*	0.77*	0.60*
	RMSE	0.24*	1.97*	37.34*	14.36*
benthic	r^2	0.93	0.92	0.89	0.91
	RMSE	0.18	0.74	25.28	6.87
all taxa	r^2	0.96	0.81	0.92	0.83
	RMSE	0.14	1.11	21.54	9.24
Shallow lakes n = 35					
planktonic	r^2	0.68*	0.89	0.79*	0.79*
	RMSE	0.46*	3.86*	1.94*	1.94*
benthic	r^2	0.96	0.91	0.96	0.96
	RMSE	0.16	2.13	0.82	0.82
all taxa	r^2	0.95	0.97	0.95	0.95
	RMSE	0.18	1.11	0.92	0.92

Table 2.2: Weighted Averaging Partial Least Square Models (WA-PLS) were based on three groups of diatoms: planktonic, benthic and all taxa.
They were executed for pH, total phosphorus (TP), total nitrogen (TN) and dissolved organic carbon (DOC) predictions in the training set of 75 lakes, deep lakes (n = 42) and shallow lakes (n = 35). Apparent root mean square error (RMSE) and r^2 accounted for the robustness and the reliability of these models. Number of component = 3. The stars * indicated a significant difference between r^2 and RMSE of planktonic algae and the two other groups.

The influence of the species number

The large variability in the number of species (planktonic or benthic) included in our predictive models made it difficult to separate the effect of the number of species from the effect of the type of taxa considered. Indeed, we identified 47 planktonic and 167 benthic diatoms. Using the complete set (all diatoms), we examined how species number influences prediction by successively deleting species at random and re-estimated a WA-PLS models at each model reduction. For pH models, the greatest lost of predictive power occurred when the number of species was below 120 (Figure 2.2), providing a preliminary threshold value when species deletion is carried at random regardless of species characteristic. We then repeated the same exercise for each group of diatoms separately.

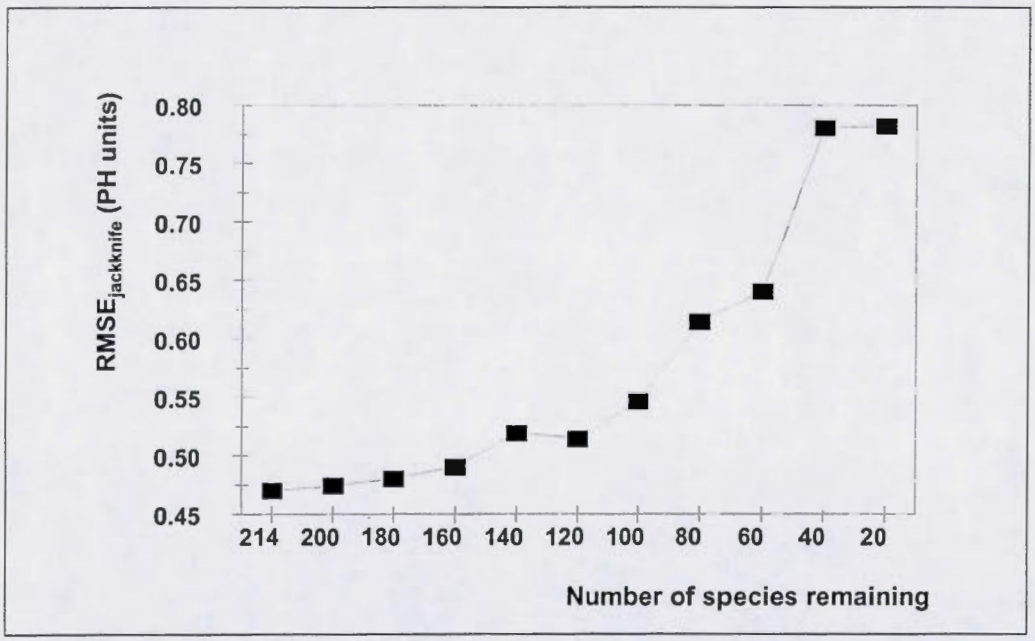

Figure 2.2 Plot of root mean square error of prediction RMSE $_{jackknife}$ for pH generated randomly from different numbers of species with regard to the type of taxa (planktonic or/and benthic diatoms).
Data sets were generated at 20-number of species intervals using a random number generator without replacement, performed ten times for each interval. The mean of RMSE $_{jackknife}$ from the ten runs and corresponding to a certain number of species, is represented

by one closed square in the plot.

For a given number of species (starting with 47, the total number of planktonic species) included in the models, planktonic diatoms yielded the better predictive potential (lowest $RMSE_{jackknife}$) in comparison to benthic species, except when the number of species dropped below 25 (Figure 2.3). The same trend was obtained for all other three variables (TP, TN and DOC). This is an important result as it argues that the higher performance of benthic taxa is essentially a species number phenomenon. While each individual planktonic species carries more predictive information when controlled for the number of species (Figure 2.3), the more numerous benthic taxa collectively generated better models (Table 2.2). It is therefore not surprising that the best models are achieved when all species are combined (Table 2.2).

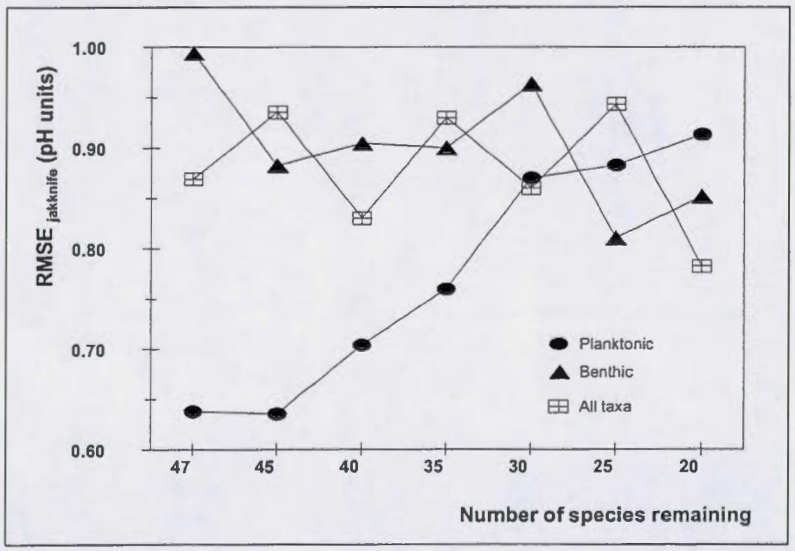

Figure 2.3 Plot of root mean square error of prediction $RMSE_{jackknife}$ for pH generated randomly from different numbers of species with regard to the type of taxa (planktonic or/and benthic diatoms).
Data sets were generated at 47 species and 5-number of species intervals using a random number generator without replacement, performed 10 times for each interval. The mean of $RMSE_{jackknife}$ from the 10 runs is indicated by the number of species corresponding.

The role of depth

Planktonic species dominate in deep lakes and comprise an average of 88 % of the diatoms relative abundance. Conversely, benthic species represent 59 % of the total abundance in shallow basins. Models built for deep lakes (Zmax >10 m) use apparent RMSE and r^2 indices because of the smaller number of lakes in models when separating the calibration set of 75 lakes into deep and shallow lakes. Benthic taxa and the group with all taxa combined produced significantly better predictions than planktonic ones for TP, TN, and DOC concentrations (higher r^2 and lower RMSE; Table 2.2). For pH, although the predictive power was not significantly different between groups of taxa, planktonic algae still produced the largest RMSE. The variable pH was the best-predicted variable independently of habitat type. The predictive power was statistically indistinguishable between models based on benthic or on all taxa combined.

For shallow lakes (Zmax < 10 m), benthic taxa and the group using all taxa produced significantly stronger predictions (lower RMSE) than planktonic diatoms for pH, TN and DOC (Table 2.2). Using only planktonic species systematically produced the largest RMSE. Regardless of the group of taxa, pH and DOC concentrations tended to be best predicted. Regardless of the depth of lakes, the deletion of benthic diatoms significantly diminished the predictive power in our WA-PLS models. Similarities of the patterns in both deep and shallow lakes suggest that lake depth does not modulate the relative importance of benthic or planktonic algae on model performance, again pointing to a species number phenomenon.

Species rarity: the role of the effective number of occurrence (N2)

Planktonic taxa were most abundant in 70% of the lakes. Dominant taxa included *Asterionella formosa*, *Aulacoseira italica* var. *subarctica*, *Cyclotella bodanica* var. *lemanica*, C. *stelligera* and *Tabellaria flocculosa*. The most widely represented benthic taxa were *Brachysira brebissonnii*, *Eunotia bilunaris*, *E. incisa* and *Frustulia rhomboides*. Hill's N2, an index of evenness which takes into account both the number of occurrences and the relative

abundance, gave higher weights to the following taxa: *Cyclotella stelligera*, *Tabellaria flocculosa*, *Aulacoseira italica* var. *subarctica*, *Achnanthes minutissima*, *Cyclotella bodanica* var. *lemanica*, *Brachysira brebissonnii* and *Frustulia rhomboides* var. *saxonica*. Sixty species may be considered as rare with a low N2 number of 1 (see Appendix 2). Because the effective number of occurrence (N2) between planktonic and benthic diatoms was significantly different (T-test, $p < 0.05$), we tried to assess the influence of selected species deletion criteria on the WA-PLS pH model. This test was done by varying the effective number of occurrence N2 for individual taxa to be included in the predictive model. We tested the influence of the effective number of occurrence N2 on the performance of models by a) successively deleting species with the lowest N2 number and conversely, b) successively deleting those with the largest N2 values.

The lowest $RMSE_{jackknife}$ occurred when all 214 taxa were included in the WA-PLS pH model ($RMSE_{jackknife} = 0.47$, $r^2_{jackknife} = 0.60$) (Figure 2.4a). The same observations were reported in Birks (1994) and in Wilson et al. (1996) when using WA and $WA_{(tol)}$ (weighted by species tolerance) models based on pH. Even if the deletion of species having $N2 < 2$ corresponded to a substantial species loss, the $RMSE_{jackknife}$ underwent very little change. There was a region of stability where the $RMSE_{jackknife}$ remained little affected, when taxa having from 1 to 9 effective number of occurrence were eliminated from the WA-PLS pH model. However, the number of species remaining in our models dropped abruptly in this range from 214 to 48 species and dropped under the critical number of species ($n \sim 120$) when $N2 > 3$.

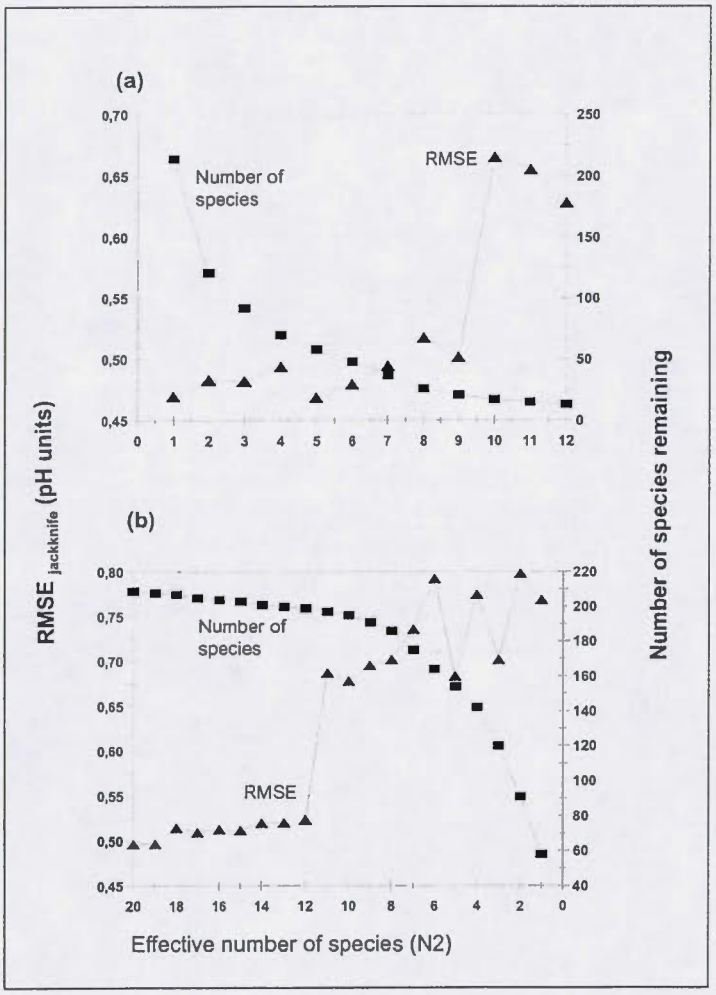

Figure 2.4 Plot showing the variation of the root mean square error $RMSE_{jackknife}$ for pH, when the effective number of occurrence (N2) changed.
We successively (a) deleted species with the lowest N2 number, or (b) deleted species with the highest N2 number. At each N2 number, the number of species remaining in the WA-PLS models was reported. In (a) when the deletion criterion was at N2 = 2, all taxa having a N2 strictly inferior to 2 were eliminated. In (b), when the deletion criterion was at N2 = 2, all taxa having a N2 superior or equal to 2 were eliminated. $RMSE_{jackknife}$ values and the number of species are represented by closed triangles and closed squares respectively.

Our second numerical experiment, where species with the largest N2 were first eliminated, also yielded interesting results. As before, the lowest $RMSE_{jackknife}$ occurred

when all taxa were included in the WA-PLS pH model (Figure 2.4a). The $RMSE_{jackknife}$ changes little between the deletion criteria of N2 = 20 and 12, probably because it corresponded to a minimal loss of species (only 15 species were eliminated). A rapid rise of $RMSE_{jackknife}$ occurred with taxa having an N2 effective number lower than 11. The number of species remaining was therefore greater than the critical number required for the relative stability of the $RMSE_{jackknife}$ (n ~120 species), and this until N2 = 3. The deletion of species presenting an N2 inferior to 11 continued to decrease the predictive ability of our WA-PLS models.

Very similar trends were observed for TP, TN and DOC when we tested the effective number of occurrence N2.

Species tolerance

Even if the average tolerance of planktonic and benthic diatoms for pH were similar (T-test, $p < 0.05$), the distribution was different between both groups and was especially asymetric for benthic taxa. Indeed, 40% of benthic taxa had a tolerance close to zero against 20% for planktonic species. We tried to assess whether the deletion of high tolerance species would improve model performance. We calculated tolerance only for species with occurrence higher than 3 in lakes to obtain relevant tolerance estimates. *Cymbella microcephala*, *Pinnularia braunii*, *Eunotia polyglyphis*, and *Aulacoseira perglabra* were the wider tolerance species for pH (see Appendix 1). In contrast, *Tabellaria ventricosa*, *Fragilaria brevistriata*, *Eunotia linearis*, and, *Navicula cryptotenella*, had narrow pH tolerances. To vary species tolerance for pH included in WA-PLS models, we a) successively deleted species with the lowest tolerance for pH and conversely b) successively deleted the highest tolerance species. The lowest $RMSE_{jackknife}$ occurred when all taxa were included in the WA-PLS pH model (Figure 2.5a). However, even if analyses were performed below the critical number of species (~120), there was a clear region of stability where deleting species with tolerance smaller than 0.6 pH units had little impact on the

predictive power of the model. Beyond the lower tolerance limit of 0.6 pH units, the number of species dropped under 60 and the residual error rose.

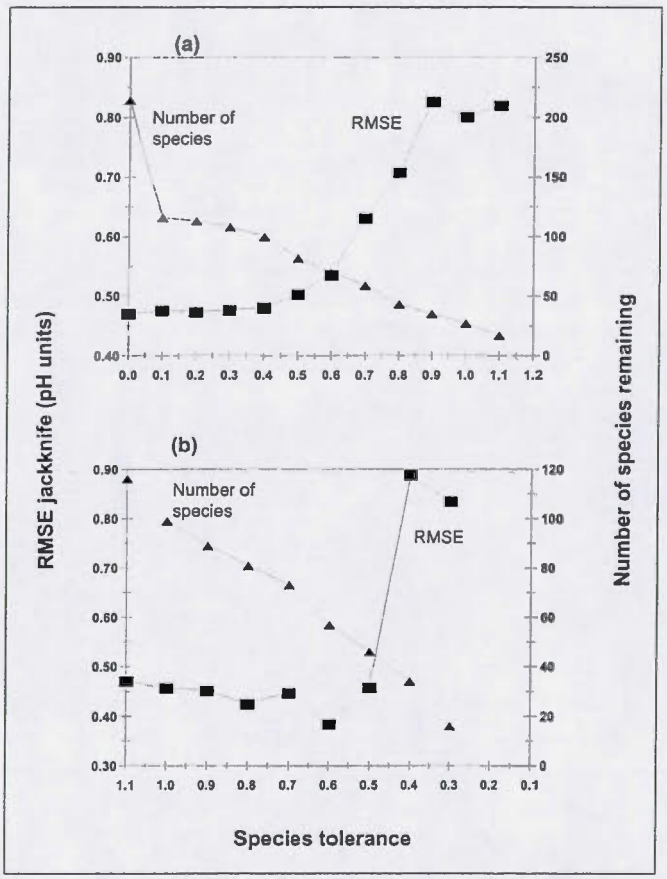

Figure 2.5 Plot showing the variation of the WA-PLS models root mean square error $RMSE_{jackknife}$ for pH, when the species tolerance changed.
We successively (a) removed species with lowest pH tolerance, or (b) deleted species with the highest pH tolerance. In (a) when the deletion criterion was at tolerance = 2, all taxa having a pH tolerance strictly inferior to 2 were eliminated. In (b), when the deletion criterion was at 2, all taxa having a pH tolerance superior or equal to 2 were removed. $RMSE_{jackknife}$ values and the number of species are represented by closed squares and closed triangles respectively.

In our next numerical experiment, higher pH tolerant species were eliminated first (Figure 2.5b). Although small in magnitude, there is a trend for a decreasing $RMSE_{jackknife}$ when species of high tolerance are removed up to an upper tolerance limit of about 0.6. Past this threshold value, the number of species remaining was very small (less than 40) and the prediction error consequently rose very rapidly. The best model (in an absolute sense) was achieved when species of WA tolerances of 0.6 or greater were removed (n = 57) (figure 2.5b).

Discussion

Contrary to our expectations, pelagic taxa, i.e. those diatoms that are in direct contact with the measured environmental characteristics of interest, are less apt to yield powerful predictive models than benthic ones. This was true for all variables considered in this study. However, once we accounted for the number of species, we found that planktonic algae showed the best predictive power. Therefore, while individual planktonic species bring more useful predictivre information than individual benthic species, on average, the latter group nevertheless produced better models because the benthic habitat harbors a much richer and more diverse diatom flora than the water column. This also explains why combining all taxa regardless of their habitat procures yet better models, with the lowest $RMSE_{jackknife}$.

Siver (1999) successfully developed transfer functions based solely on planktonic diatoms but he restricted his analysis to lakes (n = 46) with greater than 50% planktonic diatoms. Unfortunately, he did not test whether including benthic taxa as well could develop even more effective models. To our knowledge, no other study has examined this question of the effect of species deletion on the basis of habitat type (planktonic and/or benthic) on model performance.

The results presented here indicate that benthic algae do respond, directly or indirectly, to changes in open-water chemistry. However, for pH and nutrients, particularly phosphorus, the open-water environment can have concentrations an order

of magnitude lower than that experienced at the sediment/water interface, where benthic taxa live. One could argue that the benthic and planktonic habitats being physically juxtaposed (Blumenshine 1997), they must show some chemical correspondence even if the strength of the planktonic-benthic coupling may vary among systems, depending on topography and depth. This planktonic-benthic coupling also generates the potential for several modes of interaction. For example, some studies also demonstrated that benthic algae are competitively depressed by planktonic ones (shading) in eutrophic lakes suggesting a negative and indirect relation between benthic and pelagic processes (Hansson, 1988). Altough the exact mechanism by which benthic algae respond to changes in open-water chemistry is not clear, our results suggest links between benthic and planktonic diatom communities with the environmental variables selected.

The deletion of rare species (with low N2 number) had little impact on the performance in the WA-PLS pH model. In the training set, most species with low N2 number also had very low relative abundance at each sample site (significant correlation = 0.4, $p < 0.05$), and probably had very little weight in our WA-PLS pH models. Nevertheless, the observation of a plateau, observed where the removal of species with $N2 < 9$ had little effect on model performance is surprising, particularly in light of the large number of species that this represents (only about 50 species are left at $N2 < 9$). Birks (1994) showed results similar to ours with little change in $RMSE_{jackknife}$ between N2 of 1 and 15. In contrast, the plateau was much narrower in Wilson et al. (1996) where WA and WA(tol) models were approximately constant only within N2 values of 1 to 3 perhaps because the parameters (optima and tolerances) of these rare species are necessarily poorly estimated. The rapid rise in the $RMSE_{jackknife}$ observed after deleting species with N2 higher than 9 (Figure 4a), is likely due to the too low number of species remaining in our models ($n < 21$ species).

The experiment where species with a large N2 number were first deleted was also quite informative. First, very ubiquitous taxa (N2 higher than 11) apparently do not reduce the robustness of prediction by introducing noise in the calibration. Second, the sharp rise in $RMSE_{jackknife}$ when the N2 lower limit reached 11 was not a species number

effect for very few species were in fact lost. This suggests that the few species that were lost in the removal procedure were indeed very important, although probably not in a way related to their N2 values. Clearly, the effective number of occurrence N2 is not a key to the predictive importance of any taxa.

Is tolerance an important attribute?

Our observation that deleting species of narrow tolerances did not degrade the model until too few species remained is an important result because it contravenes some fundamental paleolimnological approach precepts, i.e., that species with a narrow environmental niche are particularly important. In our data set, as in many others, taxa with narrow tolerances are often rare taxa, and one can therefore question whether the estimated tolerance is small because the species is truly confined to specific environmental conditions or because the tolerance was so poorly estimated. Statistically, given two species of identical tolerance but of differing rareness, the probability that, by chance, the "rare" species will be deemed of narrower tolerance than its "frequent" counterpart is much greater than the reverse. However, in our case, the distinction is actually of little practical value because a) the relation between rarity and tolerance is likely to remain in future data sets as well, and b) our study clearly shows that no predictive power is lost when 75% of the species (those with the lowest tolerance) are removed. We suggests that rare species have poorly estimated optima and that this may explain the reason they are not very useful in predictive models. The reverse experiment (deleting wide tolerance species first) is incongruous in that it showed essentially the same results: most species are not important to the prediction and their importance does not appear to be related to their tolerances. The only difference is that species with wide tolerances were shown to actually hinder predictive success or robustness; by deleting highest pH tolerant species we obtained the lowest RMSE jackknife of all (0.38 pH units). Combining these two numerical experiments on species tolerances clearly cast some doubt on the long-held view that species tolerance is a key attribute in inference models.

Conclusion

The different findings of this study are puzzling. On the one hand, the relative performance of benthic versus planktonic diatoms suggest that the more species included in the model, the more information is bundled in the model and the better is its predictive power. On the other hand, our species deletion experiments clearly show that most do not contribute in the predictive power in the models and that some actually hinder model performance. While their ability to hinder performance seems related to their ubiquity, their importance can not be attributed to either their effective occurrence nor to their tolerance, at least in our data set. Very similar conclusions based on an entirely different modeling approach were reached by Racca et al. (accepted). However, the question remains entirely open as to what are the characteristics of a species that make it important in a predictive model. Our recommendation at this point is that, until this question is answered, the safest procedure is to include every taxa. From an ecological point of view, including all species would capture all the ecological signal and would ensure the best possible analogues in downcore reconstructions.

Acknowledgments

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Chapitre III

Effect of wildfires on diatom changes in Christina Lake over the last 1000 yrs (Alberta, Canada)

Canadian Journal of Forest Research

accepté

Aline Philibert, Yves T. Prairie et Ian Campbell

Résumé

L'impact des feux de forêt a été examiné lors d'une étude paléolimnologique sur Christina Lake qui se situe dans la forêt boréale mixte du nord de l'Alberta (Canada). Les assemblages de diatomées ont été comptés et identifiés dans les horizons sédimentaires avant, pendant et après chaque événement de feu associé à une quantité plus importante de charbon dans le sédiment. L'abondance totale des diatomées ainsi que le rapport des taxa benthiques sur planctoniques augmentent lors de chaque évènement de feu, mais aucun impact sur la richesse n'a pu être décelé. En général les évènements de feux influençaient les communautés de diatomées sur une période variant de 1.5 à 5 ans. Parmi les facteurs qui présentaient une influence non négligeable sur les assemblages de diatomées, la compétition inter-spécifique apparaît être la clé dans la variation de l'abondance relative de certains taxa.

Abstract

The impact of forest fires on a boreal lake ecosystem was investigated in a paleolimnological study of Christina Lake, located in the mixedwood sub region of the boreal forest in northern Alberta (Canada). Diatom assemblages were examined below, within, and above charcoal–rich horizons in a sediment core, which represent local fire events. The total diatom abundance as well as the benthic: planktonic ratio increased during fire, but no detectable impact on taxa richness was observed. Diatom assemblage responses to fires lasted less than 5 years. However, among significant factor in the diatom community to fire, inter-taxa competition appears to be a prime candidate in Christina Lake.

Introduction

Fire is presently the most important form of disturbance in Canada's boreal ecosystems (Bergeron 1991; Bergeron and Archambault 1993), and current climatic change models suggest that global warming may greatly increase fire activity in the western North American boreal forest. If climatic forecasts are correct, the mean area burned is likely to decrease in parts of the eastern boreal (Bergeron and Archambault 1991; Carcaillet et al. 2001a), while increasing in the central and western boreal forest (Weber and Flannigan 1997; Schindler et al. 1996; Schindler 1998). Some authors suggest that the changed fire regimes may have a greater impact on the boreal forest than the direct effects of global warming (Weber and Flannigan 1997). Because forest anthropogenic impacts on natural ecosystems and as a natural disturbance to be emulated by harvesting, a better understanding of the impact of fire on boreal ecosystems is of prime interest. Fire is known to affect the structure and composition of the forest and initiates changes in the soil processes within the catchment, inevitably influencing the lakes embedded in the forest mosaic. By modifying the hydrology and the chemistry of catchments, fire can alter mineral, nutrient and organic inputs into aquatic systems (Schindler et al. 1980; Bayley et al. 1992a; Beaty 1994). Most studies of fire impacts on aquatic systems are unfortunately of short duration, and most are without pre-burn data (e.g. Carignan et al. 2000; McEachern et al. 2000; Planas et al. 2000). Paleo-reconstructions of environmental change, while not as reliable as direct measurements, have the advantage of providing long-term records, are amenable to pre versus post-burn comparisons, and also provide a measure of temporal variability in lake response to environmental perturbations.

The literature contains contradictory results in studies of fire impacts on aquatic systems (e.g. Bayley et al. 1992a; Rhodes and Davis, 1995; Korhola et al., 1996) depending on the regional environmental conditions. Given the paucity of long-term studies in forested peatland dominated systems, we used diatoms to reconstruct past

limnological condition changes in a sediment core of Christina Lake (Alberta), where the fire history of the catchment has been studied by Laird and Campbell (2000). Our objective was first to examine whether trends towards greater total diatom abundance and lower taxa richness during fire events, as described in a similar study in eastern Canada (Enache and Prairie 2000) were also detectable in Christina L. We also examined the time to recovery after fire, to compare it with estimates for other boreal regions (Carignan et al. 2000; Enache and Prairie 2000; Planas et al. 2000). Second, because charcoal inputs into lakes can dramatically increase after fire disturbances, we tested whether the benthic: planktonic taxa ratio varied with fire, hypothesizing that the very low tolerance of planktonic to low light conditions could produce a decrease in the relative abundance of planktonic forms during episodes of high charcoal abundance.

Study site

Christina Lake (55° 40' N, 111° 90' W) is 2.3 km^2, with a drainage basin area of 1250 km^2, almost 60 times larger than the lake, and an estimated water residence time of ~ 2.5 yrs. The lake is fed by six permanent inflowing streams (Figure 3.1), and is composed of three basins with maximum depths of 26, 33, and 24 m from east to west (Bradford 1990). The 33 m deep middle basin contains continuously laminated sediments (Laird and Campbell 2000). Christina Lake is a mesotrophic (mean TP = 16 $\mu g\ L^{-1}$), dimictic and well buffered freshwater lake, although not as hard as many prairie lakes (Bradford 1990). The lake is located in the wet mixed-wood subregion of the boreal mixedwood region. The surrounding lowland vegetation is composed mainly of black spruce (*Picea mariana*) and larch (*Larix laricina*), and peatland dominates the catchment. In upland areas, trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) are the dominant vegetation. The lake catchment was not disturbed by human activity until 1980, when oil and gas explorations began in the region. A hamlet and a recreational campground are located on the north shore of the western end (Bradford 1990). Further details of vegetation and surface geology are available in Bradford (1990) and in Laird and Campbell (2000).

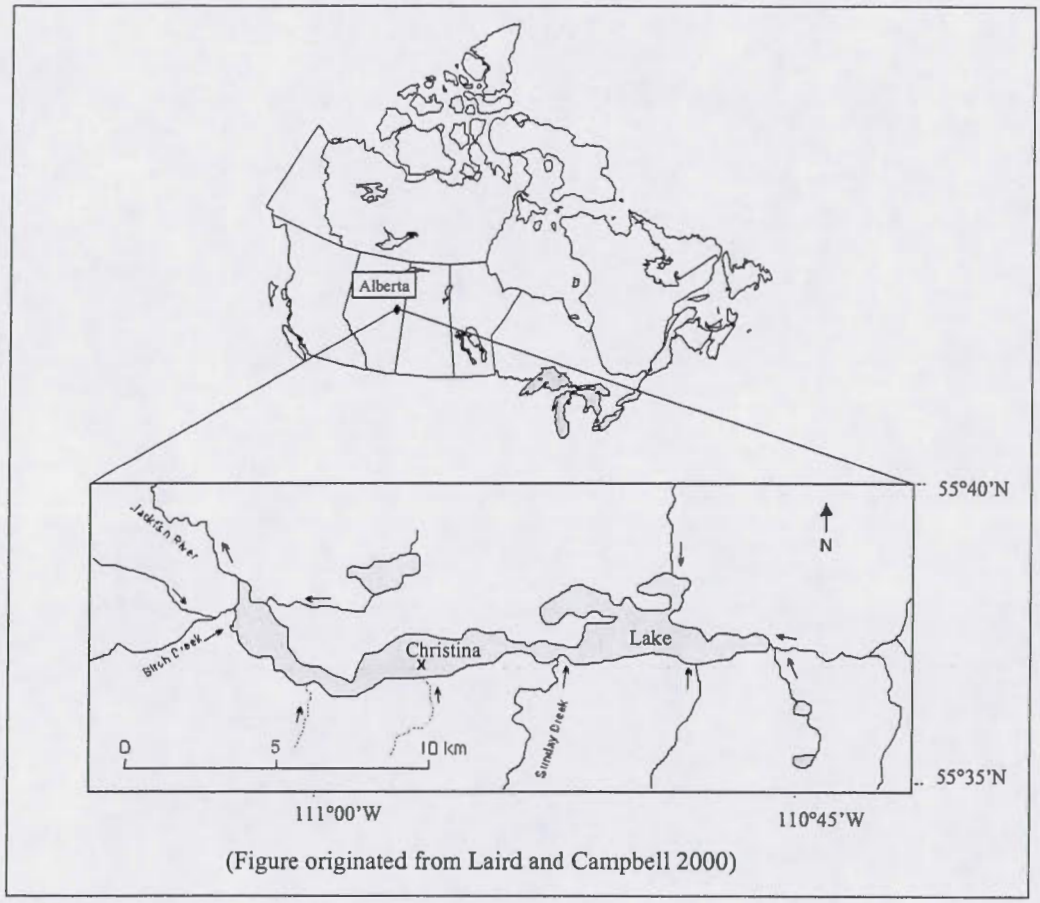
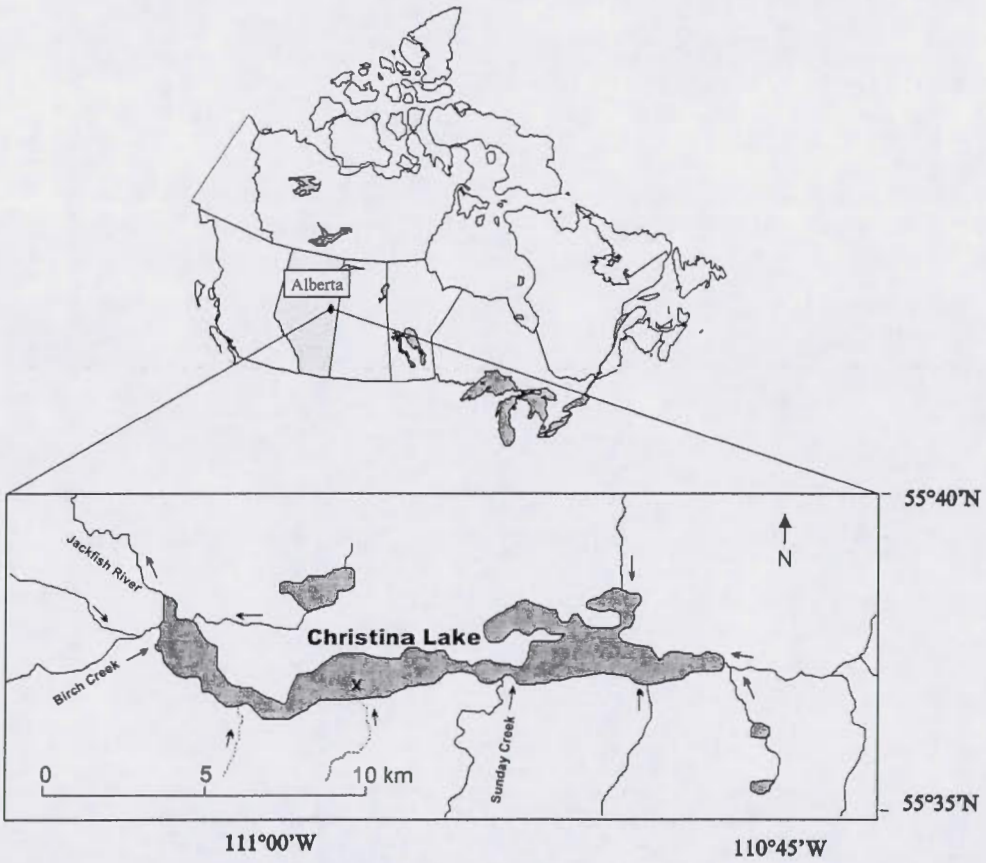


Figure 3.1 Map of Christina Lake and its location in Alberta.
The X shows the location of the extraction of the core (in Laird and Campbell 2000).

Calibration set

To determine the ecological characteristics of diatom species (optima and tolerance) of diatom species in Alberta, we constructed an appropriate diatom-lake chemistry calibration. A training set of 38 lakes was chosen from lakes in the mixed-wood region of the Boreal Plains Ecozone (Figure 3.2). Most of the calibration lakes are very shallow and do not stratify (mean depth less than 3 m). The lakes are generally eutrophic, though three of them are mesotrophic, and most are circumneutral to basic (Table 3.1). Surface

sediment samples (first cm) from the calibration lakes were provided by the Sustainable Forest Management-Network of Centres of Excellence (SFM-NCE).



(Figure originated from Laird and Campbell 2000)

Figure 3.2 Map of the training set in northern Alberta including Caribou Mountains, Buffalo Head Hills and NCE lakes.
A set of 38 lakes was selected.

variable	minimum	maximum	average	standard deviation	median
pH (units)	4.9	8.4	6.99	0.78	6.9
TP ($\mu g.l^{-1}$)	16	170.9	53.27	35.48	38
TN ($\mu g.l^{-1}$)	540	2864.5	994.44	491.9	766
Chla ($\mu g.l^{-1}$)	0.5	33.8	9.87	8.09	8.3
Ca^{2+}($mg.l^{-1}$)	0.9	46.5	13.92	11.33	8.6
Mg^{2+} ($mg.l^{-1}$)	0.04	10.9	3.73	2.98	2.5
NO_3^{2-} ($mg.l^{-1}$)	0.45	98.64	10.65	18.14	5.26
color (mg/Pt)	18.5	2884	231	473.8	101
slope (m)	0.3	6.6	2.67	1.64	2.75
vol (m^3)	15	540	161.79	135.88	105
Zmax (m)	1	33	5.92	6.27	4
Z (m)	0.7	17	2.41	2.75	1.75
DA (ha)	8.9	8208	846.1	1391.34	575
LA (ha)	8.3	216	76.97	52.11	109.7

Table 3.1: The major physical and chemical data in the 38-lake training set in northern Alberta

Material and Methods

Field and laboratory

Using a box-type freeze-corer (Swain 1973), a 100 cm sediment core was retrieved included the sediment-surface water interface from the deepest portion of Christina Lake at a water depth of 30 m in the central basin. The basin contains continuously laminated sediments. The laminations indicate a relative lack of bioturbation or other postdepositional disturbances of the sediment (Laird and Campbell 2000).

Laminations in Christina Lake are composed of regular light-colored layers of silt, diatoms and organic matter interbedded with thinner dark layers of organic matter. Vivianite (an iron hydroxyl-phosphate mineral) occurs disseminated throughout the core, and is believed to be diagenetic rather than detrital (Laird 2000). Sediment age was estimated by varve counting confirmed by ^{137}Cs decay profiles. The core was sampled at intervals of 1 cm, representing between 1.5 and 5.0 years of sedimentation, or an average of 3.5 years per cm (for more details see Laird and Campbell 2000).

Laird and Campbell (2000) used the Oregon Sieving Method, developed by Whitlock and Millspaugh (1996) to identify local forest fire events in the core, based on the abundancy of charcoal samples of size > 125 μm. Because only large fragments were extracted by this method, we presumed that the sieved charcoal curve is more representative of 'local' fire activity than 'regional' fire activity (Clark 1988). Laird and Campbell (2000) found that there was no evidence for a 'regional' charcoal signal in the results obtained for the sieved charcoal curve. Interestingly, a similar study (Capece pers. Comm.) concluded that most charcoal fragments reach the lake by stream runoff rather than by aerial transport. We can assume that fires have a lesser effect on the aquatic ecology if they do not reach the inflowing streams, and that the charcoal record in the sediments should therefore provide an indication of those fire events most likely to impact the lake chemistry and ecology. Note that it can take several seasons, even some

years, for the bulk of charcoal to be transported and finally deposited to the lake (Laird and Campbell 2000; Capece unpublished). We can expect that charcoal input could be higher to the lake during higher precipitation periods. Additional historic fire activity near the lake is documented in Delisle and Hall (1987) and in Laird and Campbell (2000) (Table 3.2).

charcoal index on the sieve curve			
depth in cm	**~ charcoal/cm²/yr**	**year of event**	***fire inferred by scars only***
17	10.9	1943.5	
18	9.11	1939	*5,5 km outside the catchment*
19	12.6	1936.5	*900 m*
20	8.88	1933	*5,5 km outside the catchment*
20-21	8.88-12.14	1931	*1km*
21	12.14	1929	*<100m*
22-21	6.43-12.14	1928	*300m*
23	4	1922.5	
24	2.89	1919	*3 km*
25-24	6.88-2.89	1916	*<100 m*
25-24	6.88-2.89	1915	*<100 m*
25	6.88	1913	*<100 m*
26-25	7.13-6.88	1911	*3 km*
26	7.13	1910	
27	6.57	1906.5	
28-27	3.14-6.57	1905	*<100 m*
28	3.14	1903	*3 km*
29-28	2.25-3.14	1901	*<100 m*
35	19.44	1872	
37	15.4	1861	
41	4.67	1844.5	
171	23.89	1043	

Table 3.2 stratrigraphic distribution of 'local' fire events and their characteristics age (from Laird and Campbell 2000).

For each 1 cm sediment interval, diatoms were isolated using standard methods (Battarbee 1973, 1986). We evaluated the total abundance of diatoms per gram of dry sediment in each 1-cm subsample from a standardized solution of *Eucalyptus globulus*. A minimum of 500 diatom valves was counted and identified. Taxonomy and nomenclature are primarily based on Krammer and Lange-Bertalot (1986-1991) and Hustedt (1930-1966).

To determine the ecological characteristics of diatom taxa (optima and tolerance) of diatom taxa in Alberta, we used an appropriate diatom-lake chemistry calibration. To this aim, a training set of 38 lakes was chosen from lakes in the mixed-wood region of the Boreal Plains Ecozone (Figure 3.2). However, ecological weighted averaging optima can be safely used to interpret diatom records when taxa occur in more than 3 calibration lakes.

Statistical analyses

Numerical analyses of the 38-lake training set included all taxa having abundances > 1% in at least one lake. Because our training set is relatively small and due to the heterogeneity and unevenness of the aquatic environment variables in their environmental gradient, the performance of our transfer functions was low. Thus, we were largely limited to developing a qualitative study to address our hypotheses and accessory the occurrence of taxa when large enough (> 3) by using their optima.

We assessed changes in pre and postfire diatom assemblages using a multi-response permutation procedure (MRPP), based on relative abundance of individual taxa. MRPP is a non-parametric procedure for testing the null hypothesis of no difference in diatom assemblages, which we apply to prefire (pre 3 cm), postfire (post 3cm) and charcoal peak samples (period of fire event). The difference between groups is assessed by Euclidean distance. A T test statistic (using $p < 0.05$) describes the separation between two groups based on the within-group and inter-group variance. This procedure is implemented by the computer program PC-ORD version 2.0 (MJM Software Design, 1995). In addition,

minimum variance cluster analyses were performed using CONISS based on Euclidean distances (Grimm, 1987), implemented by the programs TILIA and TILIA GRAPH (1991-1993) to identify the major zones in taxa composition throughout the sediment core. Two of the most dominant taxa in L. Christina, *Aulacoseira italica* var. *subarctica* and *Cyclotella bodanica* var. *lemanica*, dominate throughout the Christina L. core. These two taxa are of little diagnostic value due their wide ecological tolerances of chemical variation in our data set. Their relative abundance changes do not follow the charcoal influx along the sediment core samples. Therefore we decided to delete them from the MRPP analysis to test the responses of the other taxa.

A correspondence analysis based on similarity and dissimilarity in diatom assemblages, was executed in order to track the trends in taxonomic composition between the Medieval Warm Period and the 20th century. This was executed using the software CANOCO version 3.12 (Jongman et al., 1987; ter Braak, 1988a, 1990b).

Richness (using the number of taxa) and total diatom abundance (valves .g^{-1} dry sediment) changes were calculated from all diatom taxa.

The ratio benthic: planktonic ratio (b:p) was determined by the percentage of relative abundance in the two groups of taxa.

The distinction between planktonic and benthic taxa in our training set was established from the literature in Krammer and Lange-Bertalot (1986-1991), and according to recommendations from algal taxonomists, including one working in the same region (see the Appendix 1 for the flora description and the "pelagic" or "benthic" appellation attributed to taxa). Some «ambiguous» taxa (such as *Aulacoseira subarctica, Asterionella formosa*, and *Tabellaria flocculosa*) may were collected in both pelagic and benthic zones in different studies (pers. Comm.).

Results and Discussion

Fire history

Three major fire events were selected from the charcoal curve (Figure 3.3a, 3.3b) and included periods of recent (1903-1918 and 1929-1948) 19th century fires (1844-1885), as well as a prehistoric fire event (~1040-1045).

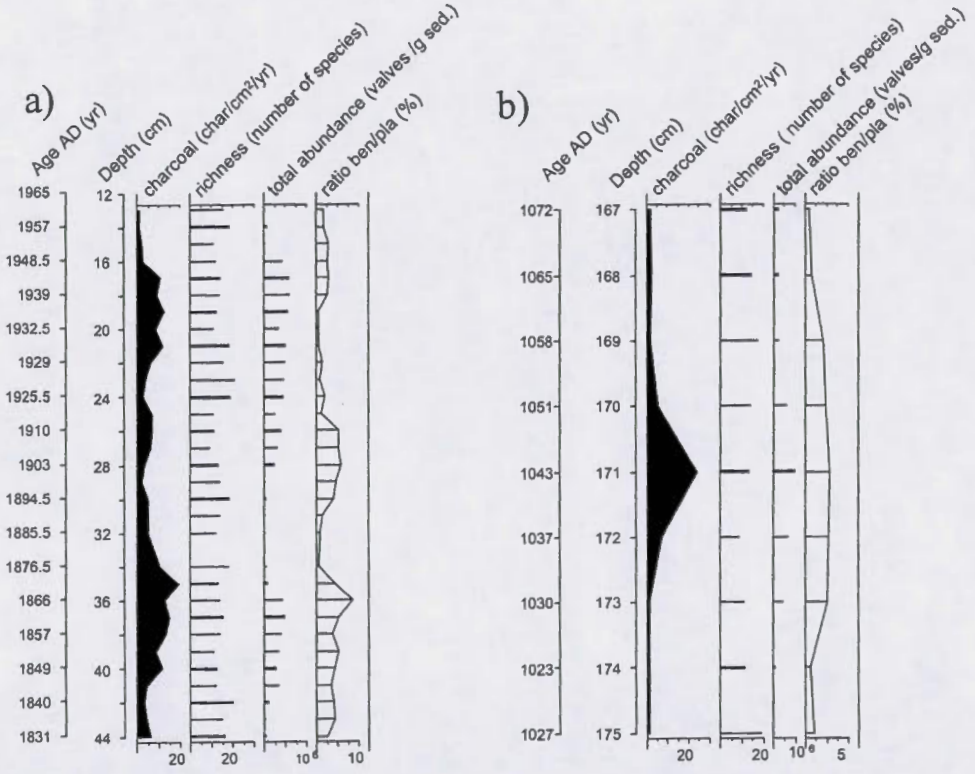


Figure 3.3 Stratigraphic diagrams of the total abundance of diatoms, species richness, benthic : planktonic taxa ratio and charcoal influx for the 1844-1885 and the 1903-1943 fire levels (a) and the fire in 1043 (b).

The youngest fire events are represented in the sieved charcoal curve as three peaks at 21 cm (~1929), 19 cm (~1936) and 17 cm (~1943) (Figure 3.3a). As shown in Table 3.2, fires in 1929 and in 1936 are also reported from fire scars, both events occurring at less than 1-km from lakeshore. Fire scars provide evidence of other fire events between 1929 and 1936, with one occurring as close as 1 km in 1931 and two outside the catchment in 1933 and in 1939 (Table 3.2). The peak around 1943 coincides with a fire very close to the lakeshore as observed in Laird (2000). We combined fire activities between 1929 to 1948 as a single fire "event", as the close timing of fires likely meant continuous charcoal influx to the lake, and thus continuous impact on lake chemistry over that period. A slight increase in charcoal concentrations is reported on the curve between 1903 and 1918 as shown in Figure 3.3a, this may be due to a couple of fires occurring during this period identified by scars or documented historic fires (Table 3.2). Because of the close timing of fire disturbances, we again treated the three charcoal peaks of 1849, 1861, and 1872 as a single fire "event" (Figure 3.3a). The 1040-1045 fire event is a single peak in the charcoal curve, and may represent a single fire or a number of fires over a short time span (Figure 3.3b).

Dominant taxa downcore

Most assemblages have about 15 diatom taxa (at least one percent of relative abundance) with a maximum of 21 around and a minimum of 9 at ca. 1035. The two dominant taxa in relative abundance, *Aulacoseira italica* var. *subarctica* and *Cyclotella bodanica* var. *lemanica* are planktonic, although more than 80 % of the taxa identified are non-planktonic. The most common benthic taxa are *Fragilaria construens* var. *binodis*, *F. construens* var. *venter*, *F. leptostauron* and *Frustulia rhomboides* var. *saxonica*. Diatom preservation was good from 11 to 46 cm, but there is some evidence of frustule deterioration from 165 to 175 cm, corresponding with the older fire around 1040-1045. Detailed characteristics of all diatoms, occurring at least at one percent of relative abundance at a minimum of one lake in the training set, are in the Appendix 3.

Impact of fires on diatom total abundance and richness

Whereas the correlation between total diatom abundance and the quantity of charcoal was significant and positive ($p < 0.001$), no relationship was observed between fire events and diatom richness (number of taxa) (Figure 3.3a and 3.3b). In all cases prefire and postfire strata had lower diatom abundances than fire events (Figure 3.3a and 3.3b). During the 1929-1948 fire event, diatom relative abundances increased as much as 20-fold, with an average increase of 3-fold for the most common taxa (Figure 3.3a). The slight increase in charcoal influx which occurred between 1903 and 1928 coincided with an increase in total diatom abundance as well (up to 15-fold). However the increase in total diatom abundance seems to start a few years before. Total diatom abundance increased up to 15-fold compared to prefire strata in the 1844-1885 events (Figure 3.3a), and roughly 6-fold in the 1040-1045 event (up to 19-fold in the single sample at the charcoal peak (Figure 3.3b). The greater total diatom abundance during fire suggests that fire results in higher diatom productivity. This agrees with the results of Enache and Prairie (2000) who conclude that fire levels are characterized by high total diatom abundance, however, they also found decreased taxa richness which is not observed in Christina Lake. For each fire event, the recovery time for total diatom abundance was equal or less than the time covered by 1 cm of sediment (a maximum of 5 years). This recovery time was much more rapid than found by Enache and Prairie (2000) who inferred recovery times between 13 and 16 years in Quebec boreal forest lakes.

Impacts of fire on the ratio benthic/planktonic taxa

Throughout the sediment samples, the benthic to planktonic taxa ratio (b:p) ranged from 0.07 to 1.7 with an average of 0.58 (median: 0.52) showing a dominance of planktonic taxa. The percentage of benthic taxa, in terms of relative abundance, significantly (t-test analysis, $p < 0.05$) increased during fire events when compared with pre and postfire events. From Figure 3.3a and 3.3b, the b:p ratio implies statistical significant and positive correlation with charcoal concentration. During each fire event

the b:p ratio increased, with the exception of the two fire peaks occurring between 1931 and 1939. Although these fires did result in an increase in charcoal deposition in the lake, they occurred at least 1 km inland from the lakeshore. Also, the charcoal and other impacts on the lake may have occurred as discontinuous inputs over several years, with a corresponding weak impact on diatom communities. The estimated charcoal catchment area of the 1943 fire shown in Laird (2000) confirms that the fire occurred at the shoreline of the basin. The rise in b:p between 1895 and 1912 may be mostly related to fires occurring between 1903 and 1919 from historic data, or may be related to wind stress and turbulence involving mixing in the water column.

One impact of charcoal influx into the lake after fire can be the effect of floating and suspended particulates on light availability. Because planktonic diatoms are probably not as tolerant to low light levels as benthic taxa, which are likely adapted to reduced and variable light levels, the input of charcoal from the streams and from the atmosphere should favor of benthic taxa. The positive response of *Tabellaria flocculosa* (planktonic) to fire disturbances, and its fluctuation in opposition to *Fragilaria crotonensis* (planktonic) and *Stephanodiscus niagarae* (planktonic), may be due either to different ecological optima for environmental variables, to inter-specific competition or also may be related to other factors such as food-web variations.

Changes in diatom assemblages after fire

Two taxa (*Aulacoseira italica* var. *subarctica* and *Cyclotella bodanica* var. *lemanica*) dominate throughout the Christina L. core and together comprise more than 50% of the total diatom abundance. These two taxa are of little diagnostic value due to their ubiquity in the calibration set and their wide wide ecological tolerances of chemical variations in our data set.

Variation in diatom composition was significant between prefire (or postfire) and fire disturbance for all three fire events (Table 3.3).

comparisons of levels:	prefire-fire	postfire-fire	prefire and postfire-fire	prefire and postfire
Fire 1 (from 1929-1948)				
T values	-2.88	0.497	0.398	0.497
probability (p)	0.015	0.36	0.57	0.36
R	0.1416	0.043	0.02	0.043
Fire 2 (from 1844-1885)				
T values	-5.99	-5.473	-7.24	-2.851
probability (p)	0.0005	0.0009	0.0002	0.022
R	0.367	0.302	0.3	0.467
Fire 3 (around 1043)				
T values	-2.973	-3.21	-4.4	-1.94
probability (p)	0.0159	0.014	0.005	0.04
R	0.514	0.33	0.373	0.102

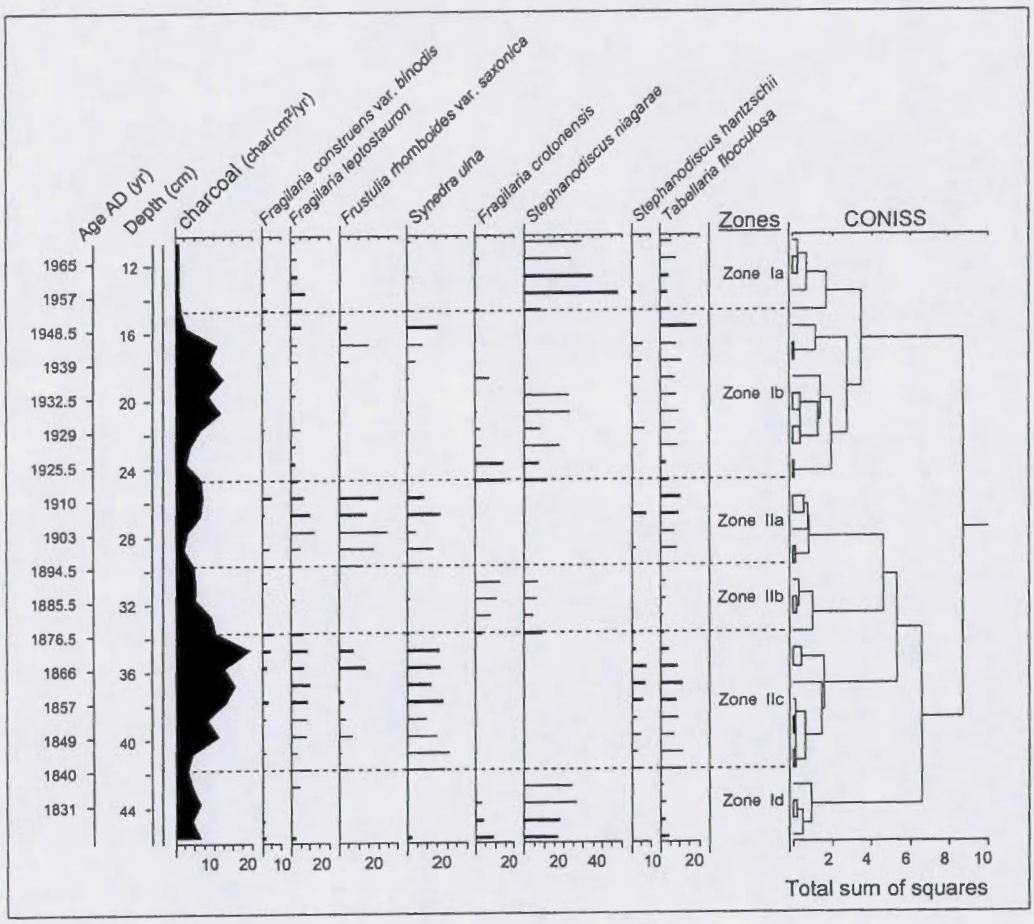
Table 3.3 Test statisctic describing the separation between the groups.
The average within-group distance is compared with the inter-group distance.
Euclidean distances are considered.
R= 1- ratio (within-group/inter-group) distance
Rmax = 1 when all items are identical withing groups
R < 10 when more heterogeneity within groups than inter-groups

Except for the 1929-1948 event, prefire and postfire diatom assemblages were similar. During the 1929-1948 event, changes in diatom assemblage coincided just before the peak of 1943 at around 1940, which we know reached to the lakeshore (Laird 2000). While both planktonic taxa *Stephanodiscus niagarae* and *Fragilaria crotonensis* disappeared, there was a strong increase in *Synedra ulna* (benthic) and to a lesser extent in *Tabellaria flocculosa* (plankonic) and in *Fragilaria leptostauron* (benthic). The event coincided with the appearance of *Frustulia rhomboides* var. *saxonica* (benthic) (Figure 3.4a zone Ib). The absence of diatom change during the fire peaks of 1929 and 1936 could be due to the

fire location within the catchment (Figure 3.4a zone Ib). It remains possible that this absence originated from a non response of diatoms to fire or also to the season of disturbance (dry season).

In 1913, 1915 and in 1916 three fires occurred less than 100 m from the lakeshore. Even though the increase in charcoal concentration was less than resulted from other fire events, this short period seems to correspond with changes in diatom assemblages, which start a few years before around at 1895 (Figure 3.4a zone IIa). Again, *Stephanodiscus niagarae* and *Fragilaria crotonensis* disappeared but *Fragilaria leptostauron*, *Frustulia rhomboides* var. *saxonica* and *Synedra ulna* appeared (Figure 4a zone IIa). This event was also accompanied by an increase in *Tabellaria flocculosa*.

During the 1844-1885 period, diatom assemblages were marked by a great relative abundance in *Fragilaria leptostauron* and in *Tabellaria flocculosa*, and by a low relative abundance in *Frustulia rhomboides* var. *saxonica*, *Stephanodiscus hantzschii* and in *Synedra ulna* (Figure 3.4a zone IIc). However, taxa such as *Fragilaria crotonensis*, and *Stephanodiscus niagarae* were disappeared (Figure 3.4a zone IIc).


Age AD (yr)
Depth (cm)
charcoal (char/cm²/yr)
Fragilaria construens var. binodis
Fragilaria leptostauron
Frustulia rhomboides var. saxonica
Synedra ulna
Fragilaria crotonensis
Stephanodiscus niagarae
Stephanodiscus hantzschii
Tabellaria flocculosa
Zones
CONISS
1965
1957
1948.5
1939
1932.5
1929
1925.5
1910
1903
1894.5
1885.5
1876.5
1866
1857
1849
1840
1831
12
16
20
24
28
32
36
40
44
Zone Ia
Zone Ib
Zone IIa
Zone IIb
Zone IIc
Zone Id
10 20
10 20
20
20
20
20 40
10 20
2 4 6 8 10
Total sum of squares

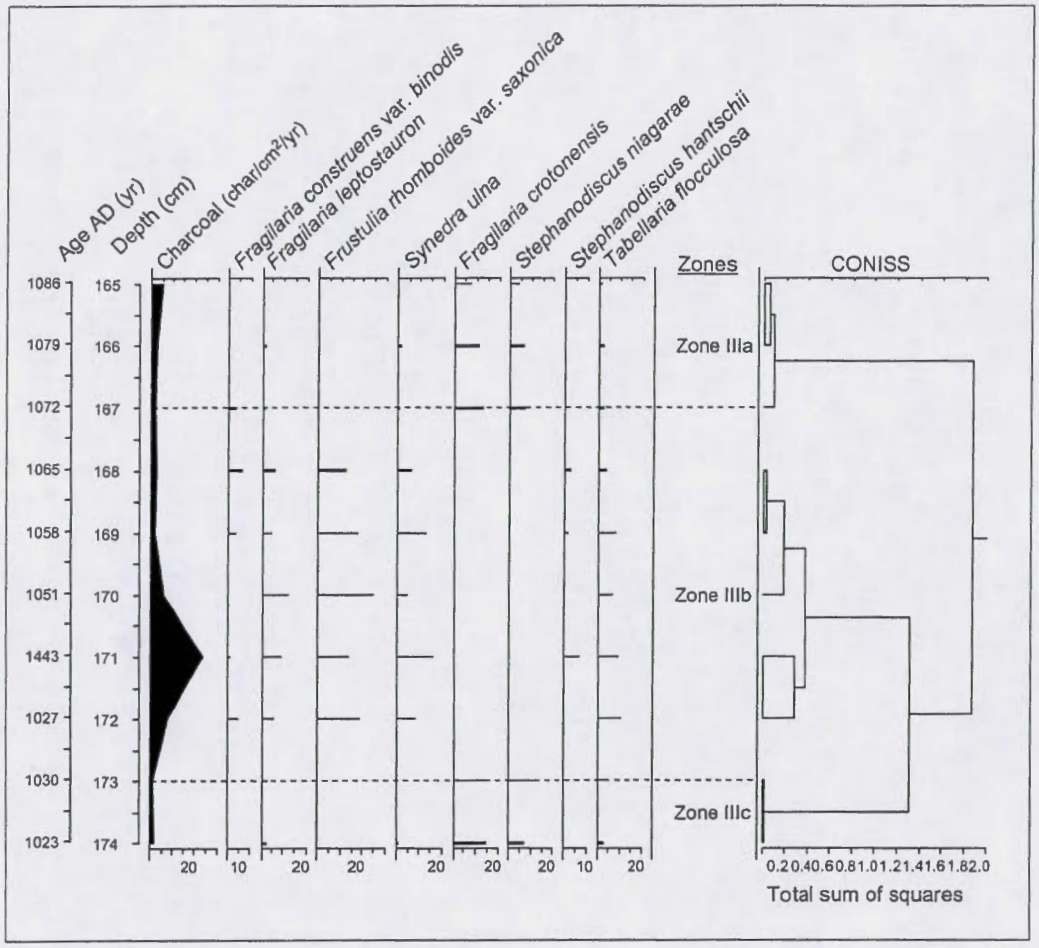


Figure 3.4 a et b Stratigraphic diagrams of the relative abundance for main diatom species, charcoal concentration for the 1844-1885, the 1903-1919 and the 1929-1943 fire levels (a) and the fire in 1043 (b).

The onset of the oldest 1040-1045 event saw a significant change in diatom taxa (Table 3.3), and this was largely reflected by increases in relative abundance in *Fragilaria leptostauron*, *Frustulia rhomboides* var. *saxonica*, *Synedra ulna* and by *Tabellaria flocculosa* that become abundant (Figure 3.4b zone IIIb). Conversely, *Fragilaria crotonensis* and *Stephanodiscus niagarae* disappeared (Figure 3.4b zone IIIb). Even if the recovery time was less than the time frame covered by 1 cm of sediment (a maximum of 5 yrs) for the other fire event, the delay after the fire 1040-1045 event was as much as 29 yrs.

Generally, the impacts of this event on diatom assemblage were not easy to interpret. This may be due to the poorer preservation of diatoms. Interestingly, the fire event 1040-1045 fire event took place in the Medieval Warm Period (Campbell 1998). Given the topography of the catchment (flat) some inflowing streams likely dried out, reducing drainage of nutrients and major ions into the lake. This could explain the short response on the sieved charcoal curve in Figure 3.4 because most charcoal reached the lake by stream runoff (Capece unpublished). At the same time, decreased runoff could have increased the lake water residence time, prolonging perturbation of lake chemistry.

When considering optima for variables such as pH, TP, TN and color of planktonic taxa, which harbor systematic opposite trends along the core samples, we observed that *Fragilaria crotonensis* and *Stephanodiscus niagarae* optima did not differ significantly and consistently from those of taxa (*Stephanodiscus hantzschii* and *Tabellaria flocculosa*) (Appendix 3). It may be that optima observed are an effect of realized rather than potential niches, and therefore are less useful than might be hoped. Moreover, we have to be very careful with optima values and to wonder whether taxa are effectively truly confined to specific environmental conditions or whether their optima is poorly estimated due to the low effective occurrence of taxa in the training set (chapter II-Philibert and Prairie 2002b). The opposite trend between some planktonic and benthic taxa may be due perhaps to the fact that benthic algae may respond to light intensity and distribution in their habitat (Vadeboncoeur and Lodge 2000) and at the same time competitively depressed by planktonic ones (shading) (Hansson (1988, 1992).

Shifts in diatom assemblages throughout climatic periods

A correspondence analysis (CA) carried out on all prefire samples only gives us the opportunity to reveal changes in diatom assemblages between the Medieval Warm Period and the two last centuries. The two first axes explain 45 % of the cumulative percentage variance of taxa data. Because the ratio of eigenvalues of axis 1 on axis 2 is higher than 1, the total taxa variance is mainly expressed on the first axis. In Figure 3.5

we observe that assemblages before the fire series of 1929-1943 (fire 1) and the older one in 1040-1045 (fire 3) were more similar than with those before fire of 1903-1918 (fire 1b) and 1844-1885 (fire 2). The maximum standard deviation of 1 is expressed on the Axis 1 between prefire assemblages. Even tough the older pre fire diatom assemblages express a short period of time during the Medieval Warm Period, we can we say with precaution that the diatom community in Lake Christina has not significantly varied over the last two centuries.

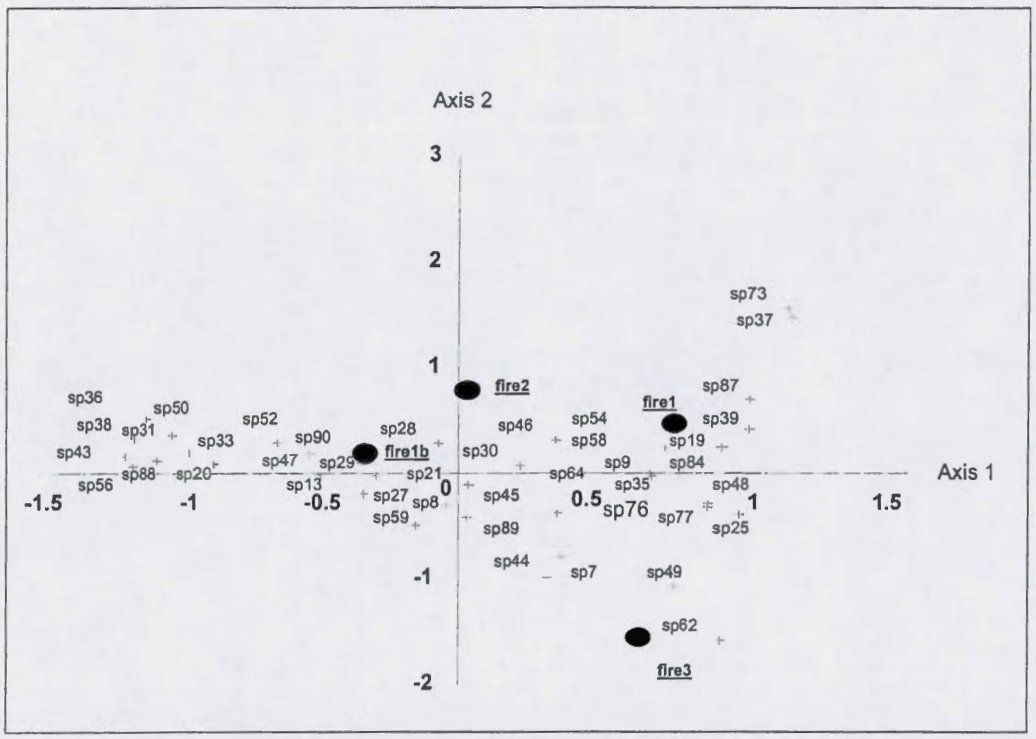


Figure 3.5 Correspondence analysis (CA) of the sediment core, showing a biplot of samples related to their similarities in diatom assemblages.
Species numbers are listed in Appendix 3. The closed circles with indicate the centroid of prefire assemblages for each fire event.

Conclusion

Some taxa such as *Fragilaria leptostauron*, *Frustulia rhomboides* var. *saxonica*, *Synedra ulna* and *Tabellaria flocculosa* do increase in relative abundance in response to fire disturbance. Conversely, both planktonic *Fragilaria crotonensis* and *Stephanodiscus niagarae* decline significantly. It remains possible that planktonic taxa may suffer from fire disturbances due to floating and suspended charcoal reducing light availability. Recovery time is in two cases of three equal or inferior to the time frame represented by 1 cm of sediment, a maximum of 5 yrs. However it took almost 30 years after the older fire 1040-1045 event. We do not have any clear evidence regarding what specific changes in geochemistry were responsible for changes in diatom assemblages during fire disturbances. Unfortunately the weakness of our predictive models prevents us from reconstructing lake chemistry with confidence. A larger modern training set which would harbor a larger and homogeneous range of environmental variables, will give us more reliable optimas and predictive models. Inter-taxa competition may explain some of the variation in diatom communities, such as the consistently opposing relative frequency changes in planktonic taxa such as between *Fragilaria crotonensis*, *Stephanodiscus niagarae* and *Tabellaria flocculosa*. Christina L. has not seen any significant change in diatom assemblages from 1000 yrs ago to the mid 20th century, indicating that environmental conditions during the Medieval Warm Period were at least broadly similar to today.

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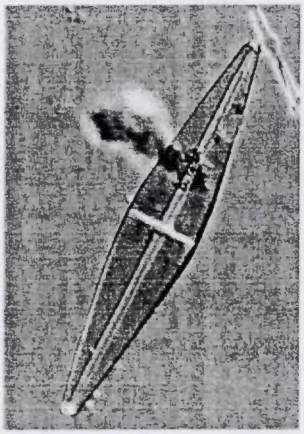

Chapitre IV

Long and short-term trends in diatom-inferred dissolved CO_2 in a small kettle lake from the Abitibi region: impact of forest fires

Soumis à Ecoscience

Philibert A. , Prairie Y.T. , Carcaillet C. , Bergeron Y. and Enache M.

Résumé

Les concentrations en dioxyde de carbone dissous (CO_2) dans l'épilimnion ont été reconstruites à partir des diatomées fossiles dans un petit lac de culot de fonte de glace au Québec (Lac Francis). Malgré une forte diminution de la concentration en CO_2 depuis les 7000 dernières années, le lac est toujours resté hyper saturé. Nous avons également observé des pics de concentrations en CO_2 d'amplitudes différentes, qui étaient clairement associés à des changements de communautés diatomiques après les évènements de feux de forêt, retranscrits par les archives de charbon dans la carotte de sédiment. Nous suggérons que la capacité des diatomées à inférer le CO_2 pourrait être à même de répondre à d'autres perspectives environnementales.

Abstract

Diatom-inferred dissolved epilimnetic CO_2, concentrations were reconstructed for L. Francis, a small glacial dystrophic lake from the Abitibi region of Quebec. We found that while there has an overall declining CO_2 trend over the past 7000 years, the lake was remained highly supersaturated. We also found significant short-term CO_2 pulses of varying magnitude and clearly associated with diatom assemblage changes following forest fires, as identified by charcoal stratigraphy. We suggest that the capacity of diatoms to infer dissolved CO_2 should be further exploited in other environmental settings.

Introduction

In hindsight, the early effects of global warming on boreal lakes were already detectable some 30 years ago (Schindler 1997, 1998). While increasing temperatures can exert significant direct effects on lake biota (Destasio et al. 1996; Schindler et al. 1996; Tilman et al. 1986), there is a growing consensus in the literature that the most profound perturbations associated with global warming trends in the boreal zone may be indirect in nature, and in particular from resulting changes in the fire frequency (Overpeck et al. 1990; Bergeron and Archambault 1993). Indeed, natural variations in fire regime are most often associated with climate changes (Clark, 1988; Swetnam 1993; Harrington and Flannigan 1993; Flannigan et al. 2001). If climatic forecasts are correct, the forest fire cycle is likely to decrease in frequency in the eastern Canada (Bergeron and Archambault 1993; Carcaillet et al. 2001a) but increase in Ontario as well as in the boreal plain of the Prairies (Schindler et al. 1996; Schindler 1998; Flannigan et al. 1998, 2001). Because fire is arguably the main source of disturbance in the boreal terrestrial ecosystem (Rowe and Scotter 1973), the expected lengthening of the fire cycle in Quebec (Bergeron and Archambault 1993; Flannigan et al. 2001) will likely modify the storage and the flux of nutrients, organic carbon and water between lakes and their catchments. While the magnitude of the lacustrine response is mostly controlled by the hydrologic regime (Fritz 1996), it is difficult to predict what the net consequences of fire for surface freshwater bodies either in contributing to or mitigating the current trend in atmospheric carbon dioxide because they critically depend on local soil, forest and groundwater characteristics. Thus, while most lakes appear to be a net source of CO_2 to the atmosphere at present (Kling et al. 1992; Cole et al. 1994), it is unclear whether this tendency will increase or decrease in magnitude with the continuing progression of global warming.

Lakewater dissolved CO_2 concentration is ultimately the net balance of both internal and external processes generating and consuming carbon dioxide. In most lakes of the Canadian Shield, and in particular in the Claybelt region of Quebec, the high

degree to which epilimnetic waters are supersaturated with CO_2 clearly suggests that most lake variations are likely driven by external processes probably by groundwater inputs as seen in chapter I (Philibert and Prairie 2002a), rather than by in-lake metabolic processes as seen in other nearby geographically regions (Prairie et al. 2002). Lakes in the Abitibi (Claybelt) region are known to have undergone significant and well-documented variations in fire regime during the Holocene (Carcaillet and Richard 2000; Carcaillet et al. 2001a). If global warming is to affect the region mostly through associated changes in fire frequency, the 7000 years of history since the regional deglaciation may provide a useful record of fire regime patterns that global warming may induce in the future. Moreover, paleolimnology provides a unique opportunity to consider multiple and interactive factors (climate and fire) that regulate ecosystem functioning and affect biota in ways not easily predicted when factors are considered independently. In this paper, we present a diatom-based inference model to reconstruct past CO_2 concentrations in Lake Francis, a small kettle lake typical of the Abitibi Claybelt region. From this reconstruction and in conjunction with fire activity derived from charcoal stratigraphy (Carcaillet et al. 2001b), we examine whether individual forest fires produce a detectable effect of lakewater CO_2 concentration and whether the temporal trends in dissolved CO_2 correspond to the documented changes in fire frequency.

Study site

Lac Francis is a small humic kettle lake located in northwest Abitibi (Quebec) near the boundary with Ontario (48° 31'35" N - 79°28'20" W) (Figure 4.1). The lake lays on flat clay plains and the surficial deposits for the area are mainly composed of glacial till formed in the Glacial Lake Ojibway before its drainage when ice retreated about 8000 cal. yrs B.P. Deglaciation of Abitibi ended with the drainage of Lake Ojibway into the Tyrell Sea at about 8,470 cal. B.P. (Barber et al. 1999).

Lac francis has a maximum depth of 6 m and a surface area of about 0.01 km^2. It develops a strong thermal stratification and an anoxic hypolimnion during summer. L.

Francis is an acidic pond (pH = 5.5), meso-eutrophic (28 $\mu g.l^{-1}$ total phosphorus), and poorly buffered (alkalinity = 70 $\mu eq.l^{-1}$). The theoretical water residence time is estimated at four months. No inflowing stream enters the lake. More details are available in Enache and Prairie (2000) and in Carcaillet et al. (2001b). L. Francis belongs to the mixedwood ecoregion in Quebec. The present day vegetation around the lake is mainly composed of *Picea mariana*, *Abies balsamea*, *Pinus banksiana* and *Betula papyfera* (Carcaillet et al. 2001a).

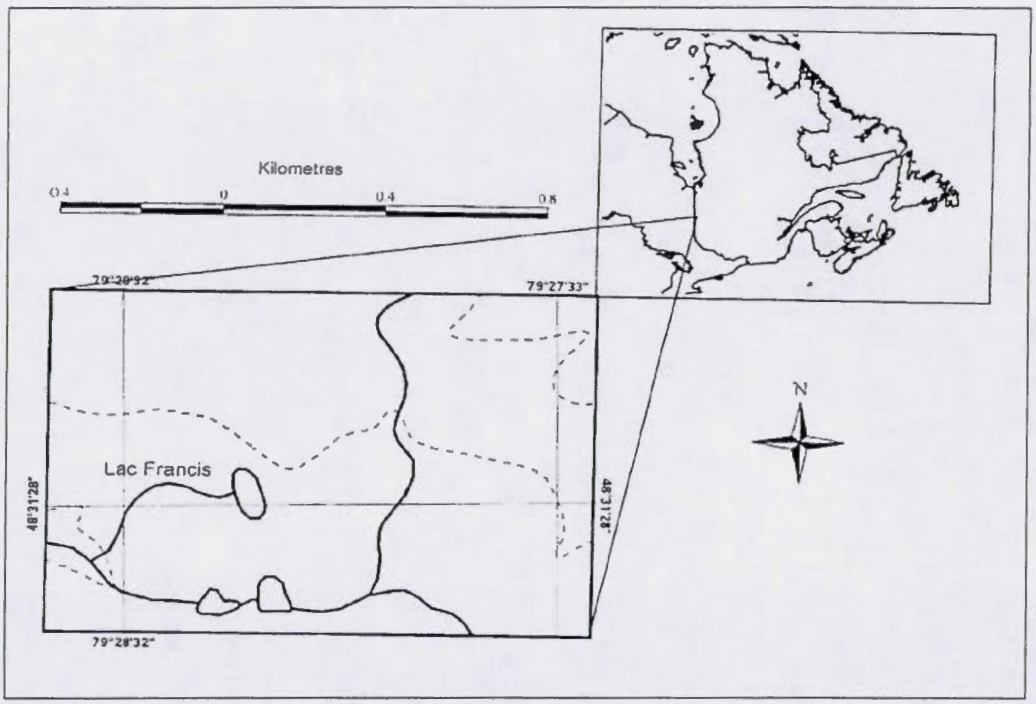

Figure 4.1 Map representing the area of Lake Francis (Abitibi, Québec) from Enache and Prairie (2000)

Training set

Reconstructions from biological fossils in lake sediments are based on the statistical relationships between regional modern diatom assemblages in surface sediments and lakewater chemistry. To this end, a survey of water chemistry and surface sediment samples was undertaken in a 76-lake training set in Quebec. This set consists of 41 lakes from Abitibi and 35 lakes from Réservoir Gouin (Haute Mauricie) (Figure 4.2). All the study lakes are located on the Precambrian Canadian Shield. The Haute Mauricie area lies on glacial till where surficial deposits are mainly composed of glacio-lacustrine fine grains and tills. In contrast, Abitibi is part of the region of Quebec dominated by clay deposits. Vegetation in both regions is typical of the boreal forest. The Haute-Mauricie and southern part of Abitibi (below 49°N) are characterized by balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) bioclimatic region, whereas the northern part of Abitibi (north to 49°N) is mainly composed of closed crown black spruce (*Picea mariana*) and mosses bioclimatic region forests (Ordre des ingénieurs forestiers du Québec 1996).

Overall, the study lakes from the two regions are fairly shallow (median maximum depth = 10 m) and small (0.01-2.31 km^2). The lakes are mostly dimictic, except for the very shallow lakes, which do not stratify. The water chemistry of the lakes is diverse and ensures coverage of a broad trophic gradient from oligotrophic to eutrophic (2.8-52 $\mu g.l^{-1}$ in total phosphorus). The lakes range from clear to darks. Abitibi lakes have a slightly broader range in DOC concentration (1.8-18.5 $mg.l^{-1}$) than lakes from the Haute-Mauricie (4.9-16.5 $mg.l^{-1}$). Similarly, the lakes in Haute Mauricie are slightly acidic to circumneutral (pH = 5.6-7.0), whereas lakes in Abitibi span a wider pH range between 4.2 and 4.8 units. Further details about the 76-lake training set are provided in Philibert and Prairie (2002) c .

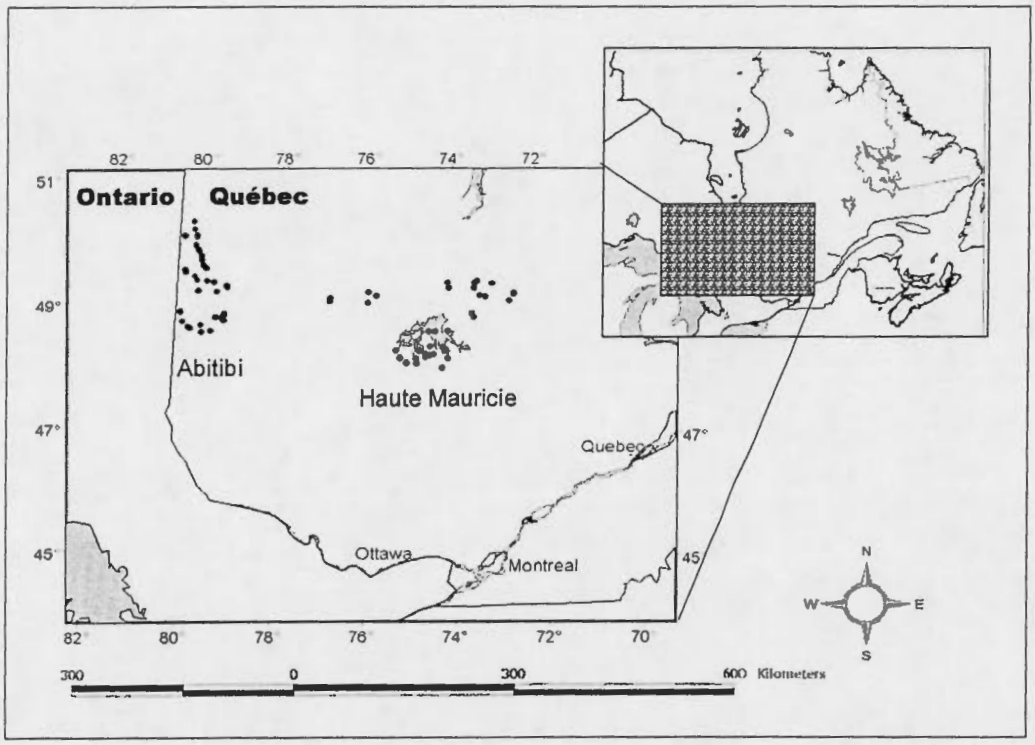

Figure 4.2 Map representing the 76-training set in Abitibi and in Haute Mauricie (Quebec).
Lakes sampled are presented by solid circles.

Material and methods

Core sampling

Using a Livingstone corer, a 3.2 m laminated sediment core was collected from the deepest portion of Lake Francis. The core was sliced into centimetre sections. At each section, a 1 cm^3 sample was taken along the longitudinal Axis of the core (for more details see Carcaillet et al. 2001a). In our study we used the macro-charcoal data. Each section was sampled for analysis of diatom, pollen and charcoal and terrestrial plant

macro remains. The chronology was based on nine AMS ^{14}C and six ^{210}Pb dating (more details are reported in Carcaillet et al. 2001a).

Charcoal analysis and chronology

For charcoal analysis, sediment samples were sieved through 150 μm mesh. Sediments were deflocculated in a 3% $Na_4P_2O_7$ solution for a minimum of two days before a gentle manual water spray was used to aid sieving. The remaining particles were bleached in a bleach water solution (10%) for several minutes to clearly distinguish charcoal fragments from dark organic matters. The total surface area of each charcoal fragment was estimated microscopically at 40x magnification using a graticule with four hundred, 0.0144 mm^2, squares and was classified into one of ten exponential size-classes: <0.1197 mm^2; 0.1197-0.2394 mm^2; 0.2394-0.4788 mm^2; 0.4788-1.0773 mm^2; 1.0773-1.9152 mm^2; 1.9152-2.9925 mm^2; 2.9925-5.9850 mm^2; 5.9850-11.9700 mm^2; 11.9700-23.9400 mm^2; >23.940 mm^2. The total surface area of charcoal in a sample was obtained by summing the mean surface area of each size-class multiplied by the number of particles in that size-class over all classes. Charcoal measurements are expressed as charcoal area concentration (mm^2 cm^{-2} yr^{-1}). More details are reported in Carcaillet et al. (2001b).

Fire chronology

In Figure 4.3, fire intervals were computed by measuring the time between two peaks of detrended charcoal accumulation rate above a given threshold (Carcaillet et al. 2001a). Local fires are assumed to generate individual peaks of charcoal above a background level derived from fires on a regional scale or from charcoal sequestered in the catchment area and its lacustrine littoral zone. The latter represents accumulation over a protracted period before final sedimentation in the deep-water sediments. Consideration only of particles larger than 150 μm excludes charcoal produced by regional burning (Carcaillet et al. 2001b) and

detrending allows removal of the remaining background signal. Detrending is based on a modeled low-frequency signal using an inverse Fourier transform. The detrended series represents the residue after subtracting the X to modeled low-frequency signal from the charcoal accumulation rate Xt. A window of 3 points running mean was found to give the best exclusion of background signal (Carcaillet et al. 2001a).

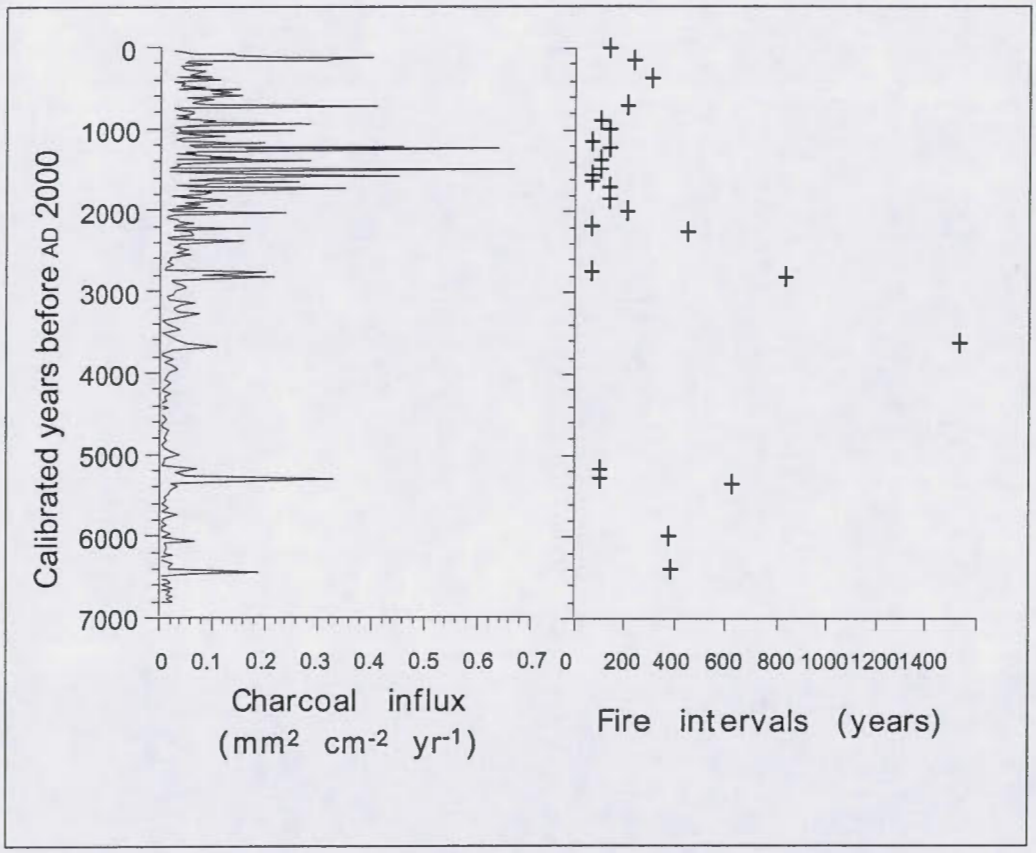

Figure 4.3 Charcoal stratigraphy and fire frequency reconstruction over the last 7000 cal. yrs B.P. (from Carcaillet et al., 2001a).

Radiocarbon chronology in Figure 4.3 indicates that the record from L. Francis covers a part of the Holocene period lasting from 7000 cal. yrs B.P. to present (Carcaillet *et al.*, 2001a, 2001b). Even if the resolution level was high (each 1cm) throughout the sediment core and permitted a reliable reconstruction of all fire events over the last 7000 years (Figure 4.3), we only selected major fire events to question our hypotheses based on fossil diatoms (Figure 4.5 and Figure 4.6).

Diatom analysis

Modern diatoms (those recovered from the surface sediments of the calibration lakes) and fossil diatoms were processed and counted following standard techniques (Smol 1983; Battarbee 1973, 1986). For each sample, a minimum of 400 diatom valves was counted and identified along random transects at a magnification of 1000x -1600x using a Leica DMR microscope. Data taxonomy and nomenclature were based on Hustedt (1930-1966); Krammer and Lange-Bertalot (1986-1991); The PIRLA Diatom Iconography (Camburn et al. 1984-1986). A detailed appendix of floristic data characteristics (optima, N2) is available in Appendix 1. The diatom floristic description was detailed for each 1 cm before and after major fire events, while a coaser analysis of 20 cm intervals was carried out between fire levels.

Numerical analyses

Correlations between diatom assemblages and limnological variables were estimated by multivariate statistical techniques and are used to derive transfer functions (or predictive models) for the reconstruction of variables from fossil remains. The details of the transfer functions are reported in Philibert and Prairie (2002a) (chapter I). The main approach is summarized as follows. A weighted average partial least squares (WA-PLS) technique was used because it takes into account both the unimodal response of diatoms along environmental gradients and the information contained in the residuals, thereby

diminishing bias (ter Braak and Juggins 1993). Significant and predictive WA-PLS models were developed for pH, CO_2, and TP (chapter I- Philibert and Prairie 2002a). All the diatom-based transfer functions were considered because they can explain directly or indirectly the causes of CO_2 changes. The analyses were carried out using a SAS/IML implementation of the WA-PLS algorithm (Prairie, unpublished program).

We used statistical procedures to verify that the calibration set provides analogs for the fossil core samples. The first approach tests that sufficient overlap existed between the calibration model and downcore diatom assemblages in terms of the relative abundance. The computer program ANALOG was used to evaluate if sufficient analogs existed between the training set and the core sample diatom assemblages (H.J.B. Birks and J.M. Line, unpublished program). The similarity coefficient we chose was the squared chord distance or DC (Overpeck et al. 1985). Confidence intervals were based on the mean minimum DC distance within the modern training set. Core samples above 95% confidence intervals were considered to have no analogs.

The second approach evaluated the degree to which the calibration set provided reliable estimates of reconstructed variables. We performed separate canonical correspondence analyses (CCA) constrained to one single explanatory variable in order to evaluate the reliability of WA-PLS models to infer each environmental variable throughout the sediment core. This was completed by calculating the squared residual distance of each core sample (passive) from Axis 1 in the CCA. Core samples with squared residual distances outside the 95% confidence were deemed as very poor fit for estimating the selected variable. More details are given in Birks et al. (1990) and these procedures have been used in similar paleoecological studies by Laird et al. (1998) and Laing et al. (1999). We also tested whether estimates of reconstructed variables accounted for a significant part of diatom assemblage shifts throughout the core, using a correspondence analysis (CA). This test analyzed the relationship between CA Axis 1 core sample scores and estimated values for each reconstructed variable throughout the core.

Results and discussion

Evaluation of model fit

The computer program ANALOG identified good analogs between the modern calibration set and downcore species assemblage in terms of relative abundance. Only one sample at depth 104.5 cm has poor analog (Figure 4.4a). This is probably due to the very high relative abundance in *Aulacoseira distans* var. *tenella* that includes more than 80 % of the all taxa at this depth. No such percentage for this taxon was found in the calibration set. In term of species, all core diatom samples (100%) were represented in the modern training set. Likewise, most of the dominant species in the core stratigraphy had high Hill's N2 values (e.g., 4.1 to 13.8; mean = 8.92) in the calibration set, suggesting that their ecology was well circumscribed and diatom-based reconstructions reliable (for more details on ecological characteristics on species see chapter I (Philibert and Prairie 2002a).

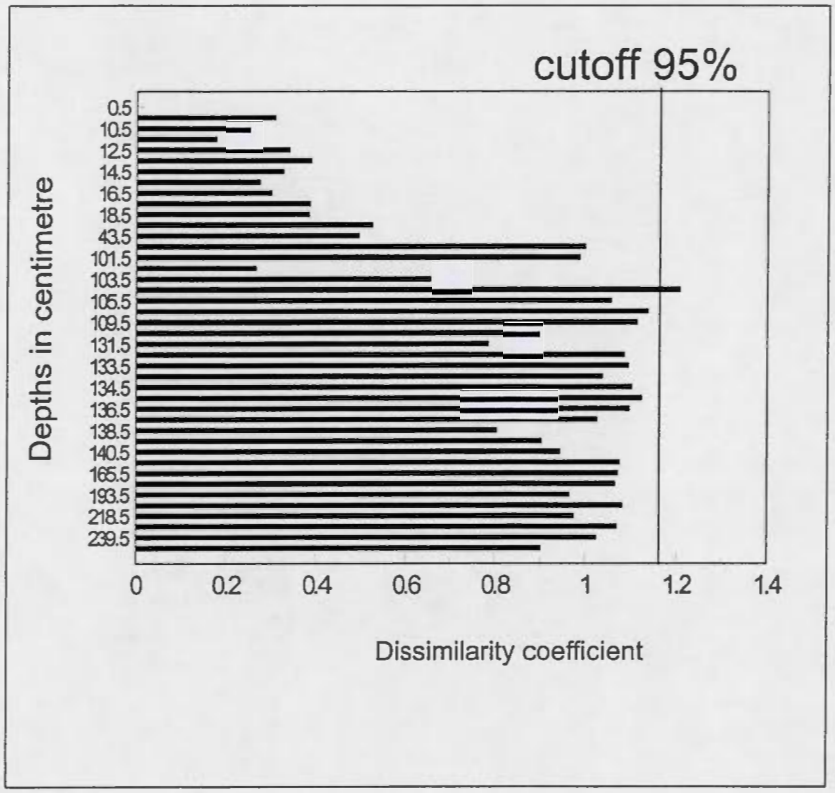

Figure 4.4a Core samples with dissimilarity coefficients (D.C.) greater than the 95% cutoff are considered to have no analogs with the modern 76-training set.

Analyses of squared residual lengths in CCAs constrained to each environmental variable CO_2, pH, and total phosphorus (TP), indicate that the reliability for each reconstructed variable when based on WA-PLS models is strong throughout the core. Indeed for each reconstructed variable, at least 70% of the core residuals fall within the 95% confidence intervals in the calibration set residuals.

The very strong relationships between CA Axis scores and reconstructed CO_2, pH and TP throughout the core (Figure 4.4b) support the idea that fossil diatom assemblages may mainly respond directly to CO_2, pH and TP changes or indirectly via factors associated with these changes.

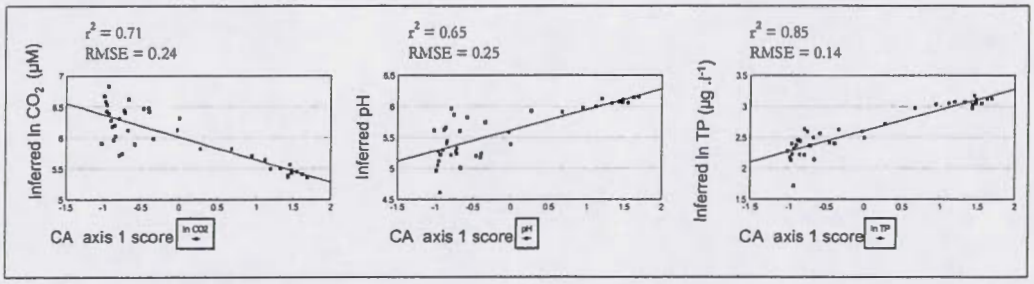

Figure 4.4b Relationship between inferred environmental values and CA Axis 1 scores a) ln CO_2, b) pH, c) lnTP

Finally the very good correspondence between the actual measured value (244 µM) and the estimated value at the sediment surface (233 µM) supports the reliability of our CO_2 WA-PLS model. The same is true for the other environmental variables with each measured value falling within the 95 % confidence interval of the WA-PLS model.

Major trend in diatom stratigraphy

A total of 71 species from 15 genera were identified in the core stratigraphy of L. Francis whereas 214 species were cataloged in the 76-lake modern training set. Only the dominant taxa are included in the percentage diagrams shown in Figure 4.5.

Between 6500 and 2200 cal. yrs B.P. (Figure 4.5 zone 3), diatom assemblages are dominated by benthic species represented by *Pinnularia braunii* and to a lesser extent by *Navicula leptostauron* and *Stauroneis angrestis.* Between 4000 and 2200 cal. yrs B.P. the planktonic taxa, *Tabellaria ventricosa* shows high relative abundances (up to 40%) although benthic diatoms still dominated the assemblages.

At about 2200 cal. yrs B.P. (Figure 4.5 zone 2), the diatom community undergoes an abrupt major shift toward dominance by planktonic species. This shift is clearly marked by the appearance of *Aulacoseira distans* var. *distans* and *A. distans* var. *tenella.* From our sampling regime a major shift occurs at about 615 cal. yrs B.P. (Figure .5 zone 1). It could have been occurred before. We observe the transfer from *Aulacoseira distans* var. *distans* to *A. ambigua*, an increase in *A. distans* var. *tenella* and a concurrent decrease in *Pinnularia*

braunii and in *A. distans* var. *tenella.* A strong increase in *Aulacoseira distans* var. *tenella* and a concurrent decline in *Pinnularia braunii* (Figure 4.5 zone 1) do coincides with charcoal peak.

Interestingly, the three major diatom-based groups coincide with the three periods of fire frequency discussed in Carcaillet et al. (2001a). Carcaillet et al. (2001a) show that a drop in mean fire interval occurred at 2200-2000 cal. yrs B.P. followed by an increase at about 1300 cal. yrs B.P. Nevertheless, the mean fire interval over the last 1300 years has remained lower than before 2200 cal. yrs B.P.

Prior to 2200 cal. yrs B.P. diatoms are dominated by benthic species. This period corresponds to low TP values. However, some shifts in dominant species indicate that limnological conditions are fluctuating during this period (between 6750 and 2200 cal. yrs B.P.). We suggest that this shift is due to the appearance of *Tabellaria ventricosa* in the planktonic taxa between 4000 and 2200 cal yr B.P. This may be related to an increase in the maximal depth (reconstructed maximal depth not represented here). The date 2200 cal. yrs B.P., which corresponds to an increase in fire frequency, is marked by a strong shift in diatom assemblages from benthic to planktonic dominant species, with the appearance of *Aulacoseira distans* var. *distans* and *A. distans* var. *tenella.* An increase in fire frequency is often initially accompanied by an export in leached and suspended material through the catchment. Then benthic algae respond to the shift in light intensity and distribution in their habitat (Vadeboncoeur and Lodge 2000). Likewise, Lac Francis changes from being oligotrophic to mesotrophic during the same period. A rise in inferred TP concentrations coincides with an increase in primary production, which can reduce light as well. Indeed, Hansson (1988, 1992) demonstrates that benthic species are competitively depressed by planktonic forms (shading) in eutrophic lakes, suggesting a negative relation between non-planktonic species and the productivity of lakes. At about 1250 cal. yrs B.P., the decline in fire frequency corresponds to an abrupt change in vegetation composition toward more balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) but lower abundance of eastern white cedar (*Thuja occidentalis*) and birches (*Betula sp.*) as reported in a similar study in Carcaillet et al.

(2001a). This shift could explain the rise in *Aulacoseira ambigua* and in *A. distans* var. *tenella* at 650 or before 650 cal. yrs B.P. (Figure 4.5 zone 1). We hypothesize that this latter shift in diatom assemblages is related to the continuous increase in TP concentrations, which in turn may have resulted from the change in vegetation within the catchment at 1250 cal. yrs B.P.

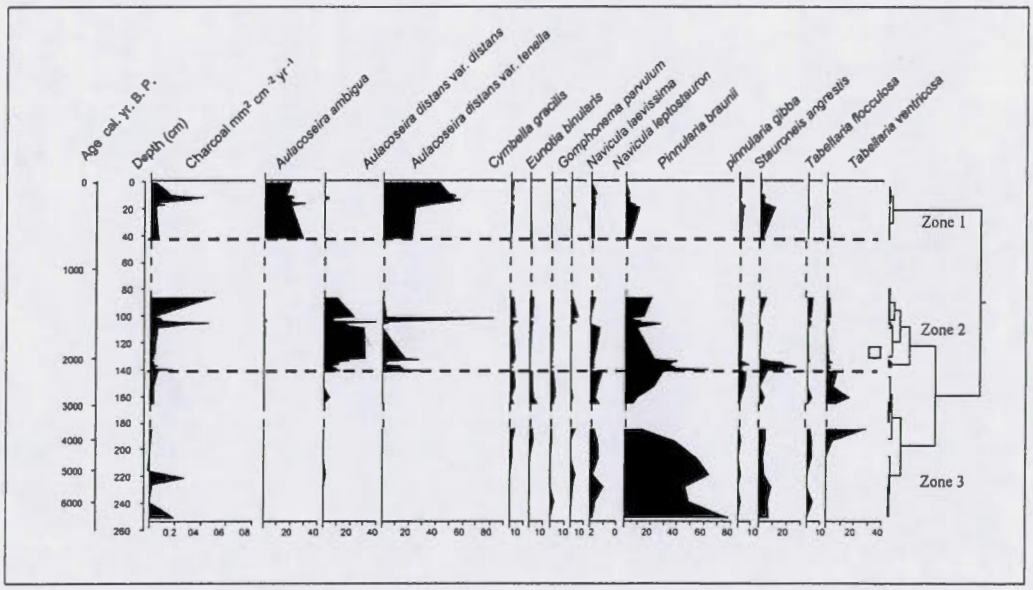

Figure 4.5 Stratigraphic diagram of the relative abundance of main diatom taxa, and charcoal concentration in the sediment core of Lac Francis.

Impacts of fire on diatom assemblages

Regardless of the major trends in diatom stratigraphy, species respond significantly and positively to fire events by increasing in relative abundance (Figure 4.5). The oldest fire around 5181 cal. yrs B.P. has an important impact on *Pinnularia braunii* with a relative increase of 20% (Figure 4.5 zone 3). The two fires occurring at 2206 and 1576 cal. yrs B.P. coincide with an increase in *Aulacoseira distans* var. *distans*, *A. distans* var. *tenella* and in *Pinnularia braunii* (Figure 4.5 zone 2). *Stauroneis angrestis* responds positively to the fire at 2206 cal. yrs B.P. During the event of 1576 cal. yrs B.P. *Aulacoseira distans* var. *tenella* reaches a huge increase of 400 %. Finally, the recent fire at 141 cal. yrs B.P. corresponds to an important rise in *Aulacoseira ambigua* and in *A. distans* var. *tenella* (Figure 4.5 zone 1). Each response of species to fire is short-lived, occupying less than one-centimetre interval of sediment. However, the lower sedimentation rate before 5000 cal. yrs B.P. impairs a reliable assessment of time recovery in diatom assemblages after the fire event of 5181 cal. yrs B.P.

Impacts of fire on inferred lakewater CO_2 concentrations

Throughout the core, reconstructed lakewater CO_2 concentrations respond positively but with different magnitudes to fires relative to pre-fire values (Figure 4.6). Fires occurring at ca. 5181, 2206 and 1576 cal. yrs B.P. show important rises in CO_2 concentrations to 793, 756 and 470 μM from prefire values of 621, 555 and 312 μM respectively (Figure 4.6 zones 2 and 3). In contrast, the younger fire at 141 cal. yrs B.P. only produced a small increase in CO_2 of 20 μM relative to prefire values (238 μM) (Figure 4.6 zone 1). This weaker response may be explained by greater moisture combined with less material drained from the catchment due to a thin layer of and maturity of the litter as proposed in Enache and Prairie (2000).

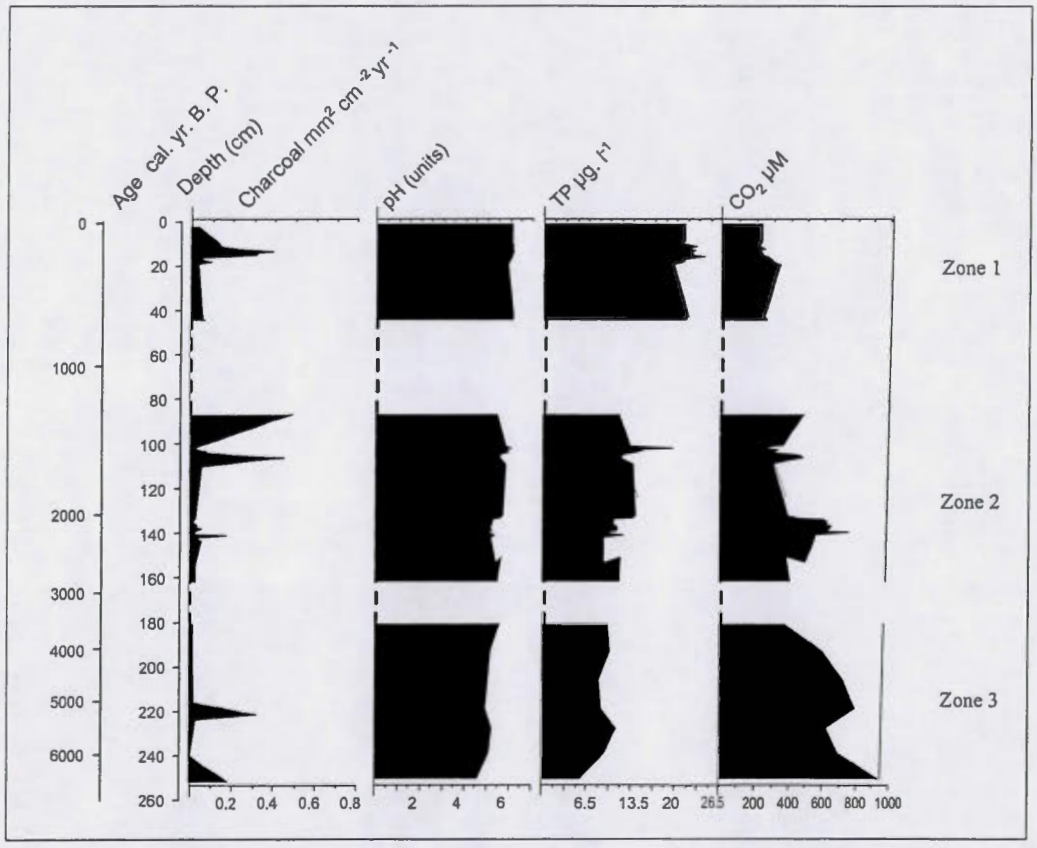

Figure 4.6 Stratigraphic diagram of the diatom-inferred values of pH, TP, CO_2 and charcoal concentration in the sediment core of Lac Francis over the last 6500 years.

To compare the relative impact of the fires on dissolved CO_2 concentrations, we normalized all diatom-inferred CO_2 values to their respective average prefire conditions. Because of the low temporal resolution before 5000 cal. yrs B.P., the older fire was not taken into account. Figure 4.7 shows that, while there is considerable variation in the amplitude of the pulse among fires, the trends are very similar: a short-lived (1 cm) peak followed by lower concentrations. As an aside, the rapid recovery after the fire-induced CO_2 pulses suggests that reconstructed CO_2 may be a good marker of fire events. Indeed, each fire event was marked mainly by the rise of relative abundance in *Pinnularia braunii*, *Aulacoseira distans* var. *distans* and *A. distans* var. *tenella*.

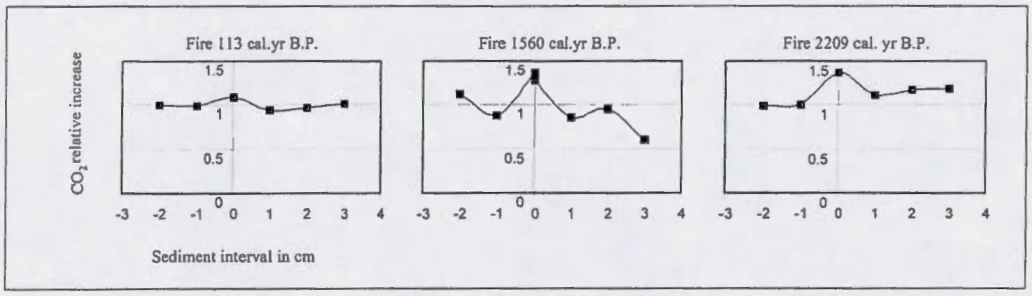

Figure 4.7 Ratio of fire and postfire diatom-inferred CO_2 on the average prefire concentrations which is indicated by the value 1 in Axis of Y.
This was realized for each one-centimeter sediment interval. -2 and -1 scores signify 2 cm and 1 cm sediment interval before the fire event respectiveley, 0 means fire event and positive values represent postfire events.

Major trends in CO_2 stratigraphy

Reconstructed CO_2 covers a wide range of values from 934 µM (prior to 6500 cal. yrs B.P.) to 233 µM (at present). Throughout the core, Lac Francis has remained highly supersaturated with CO_2 and has therefore been a continuously source of CO_2 to the atmosphere. While these values fall well within the range described by Cole et al. (1994) for lakes, they are much higher in relations to lakes in other regions of Quebec (Prairie et al. 2002). The fire-induced short-lived CO_2 pulses described above are, in fact, superimposed on this general declining trend of nearly four-fold, which is not related to the fire frequency during the Holocene.

Clearly, other factors regulate the CO_2 lakewater concentration patterns. We have argued in chapter I that the degree of supersaturation is so high in Abitibi lakes that it cannot be attributed only to in-lake processes (chapter I-Philibert and Prairie 2002a). While the exact nature of this decline remains unclear, it reflects either the gradual exhaustion of the parent material producing the supersaturation within the catchment or a decline in its transport to the lake. The hypothesis of the degradation of DOC to CO_2 is unlikely because no relationship was observed between the reconstructed DOC and CO_2 values (not presented here). However, some internal processes may be at play as well. In particular, the inferred increase in trophic status (Figure 4.6) implies greater

primary production and eutrophic lakes are known to have an autotrophic metabolic balance (del Giorgio and Peters 1994). This may have contributed to reduce the apparent CO_2 supersaturation in this lake. Indeed, the overall trend in diatom inferred dissolved CO_2 is well correlated ($R^2 = 0.88$) with inferred TP since 2200 cal. yrs B.P. (Figure 4.8) with both values following a mirror image. Several hypotheses may be considered also even if not tested. Once the Proglacial Ojibway Lake drained to the Tyrell Sea ~ 8740 years ago, clay surface deposits rich in carbonates were settled in the Abitibi region. Litle by little, organic acids from vegetal detritus may have acidified carbonates in the upper layer of soils and thus provided a possible production of CO_2 in the soil water and then into the groundwater network. Along centuries, carbonates have been progressively acidified and eliminated from upper horizons. The remaining carbonates lay on horizons C at a deeper depth, which are associated with a lower temperature and where chemical reactions are the slightest. This could explain a lower production of CO_2 from the catchment into the lake. With an ageing of soils, organics acids originated from the vegetation may have buffered from other reactions such as cationic exchanges. Another possibility will be a deccrease in oxygen concentration in the soil waters involving a decrease in the aerobic decomposition of organic matter and therefore a decrease in the production of CO_2. Also a change in the soil fauna may have drive changes in the decomposition of organic matter within the soils.

The present study shows that diatom assemblages are likely dependent on fire regime. Regardless of the accuracy of the global warming predictions, we stress the need for more studies exploring the long-term relationships between terrestrial and aquatic processes within boreal forest in order to attempt to explain the continuous decrease in CO_2 concentration.

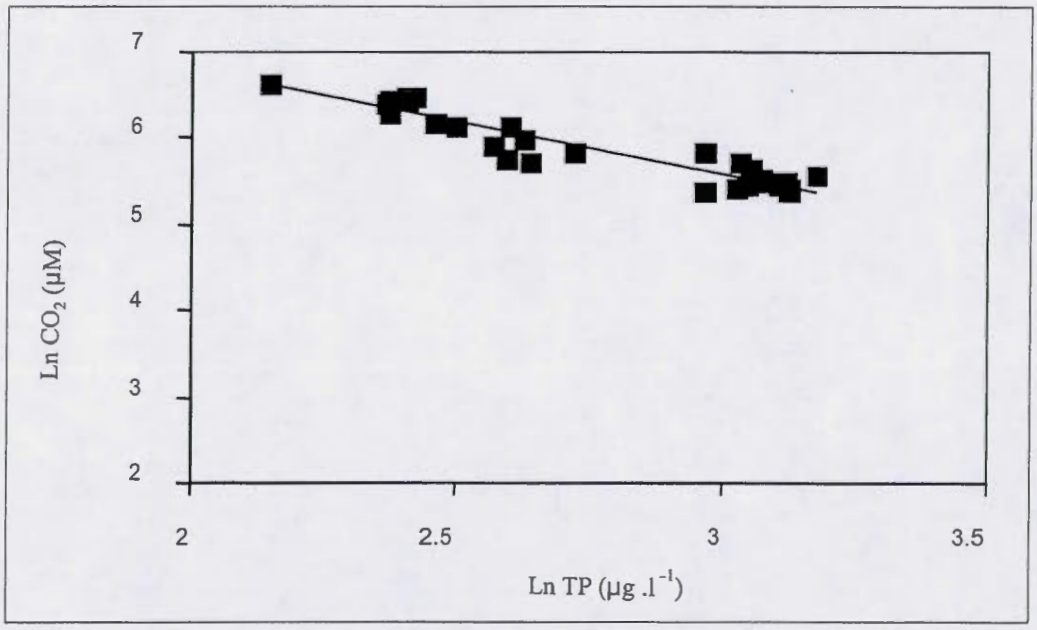

Figure 4.8 Plots of ln CO_2 versus ln TP concentrations in Lac Francis over the last 2200 years.
There is a significant linear and negative relationship between both variables of interest suggesting an influence of the trophic level on the lakewater CO_2 concentration.

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Chaptitre V

A 1200 year paleolimnological study in a small kettle lake in the *Picea mariana*-moss domain (Quebec, Canada): impacts of fires on lake biogeochemistry as inferred from diatom remains.

Journal of Paleolimnology

accept

Philibert A., Prairie Y.T., and Carcaillet C.

Résumé

Les recherches entreprises pour les effets des feux de forêt sur la chimie de l'eau sont importantes si l'on considère les changements de la fréquence et de l'intensité des feux dus au changement climatique global. En raison des différences importantes déjà observées au Québec dans la succession de végétation après feu entre les forêts mixtes et celles de conifères purs, nous avons mené une reconstruction paléoécologique à long terme des impacts des feux sur la biogéochimie du Lac à la Pessière, situé dans une forêt de conifères (pessière à mousses). Nos résultats ont été comparés avec des études réalisées en forêt mixte plus au sud. L'étude paléolimnologique a été réalisée à partir de restes de diatomées (classe: *Bacillariophyceae*) sur une période calibrée de 1200 ans afin de reconstruire les changements environnementaux d'intérêt limnologique après feux (pH, phosphore total (NT), azote total (NT), carbone organique dissous (COD) et la concentration en dioxyde de carbone dans l'épilimnion (CO_2)). Nous avons comparé la composition des diatomées et les variables reconstruites avant et après perturbation. Contrairement à une étude similaire réalisée au Lac Francis en forêt mixte, aucun changement n'a été observé dans la chimie de l'eau pendant les événements de feux à l'exception possiblement du CO_2 pour un feu. Cependant, nous avons observé un déclin de la concentration en CO_2 depuis les dernières 400 années. Les résultats suggèrent les feux des forêts de conifères auraient peu d'effets sur la chimie de l'eau du lac récepteur. Nous expliquons ces résultats tout d'abord par l'excès d'humidité et la forte épaisseur d'humus au sol qui pourraient limiter ainsi la mobilisation des nutriments et des ions majeurs, tout ceci accentué par le faible rapport bassin de drainage sur le volume du lac.

Abstract

Research on the effect of fire on water chemistry are important considering that large changes in frequency and in intensity of forest fires are anticipated as a consequence of global warming. Due to the important differences in succesionnal vegetative trends after fire between mixed-wood and coniferous-dominated forests in Quebec, we undertook a long-term paleoecological study of the impact of fires on the biogeochemistry on Lac à la Pessière, a small located in a conifer-dominated ecoregion and our results compared with similar studies done in the southern mixed-wood forest. The paleolimnological study was carried out using diatom remains (class: *Bacillariophyceae*) to reconstruct changes in environmental variables of limnological interest (pH, total phosphorus (TP), total nitrogen (TN) and dissolved organic carbon (DOC) and epilimnetic carbon dioxide (CO_2) values following fire disturbances over the last 1200 cal. years. We compared diatom composition and related reconstructed variables of limnological interest before and after fire events. Contrary to a similar study realized in mixed-wood forest in Lac Francis, no changes were observed in lake chemistry during fire events except, possibly, for CO_2 in one fire event. However, CO_2 showed a clear decreasing trend since the last 400 cal. years. The results suggest that fire-induced changes in lake chemistry are small in catchments dominated by conifers. We suggest that this may be the result of excess moisture and the thick humus layer, which likely limits the mobilization of nutrients and major ions even during a fire event.

Introduction

A recent conceptual approach hypothesizes that timber harvesting (clear-cutting) has similar effects to those of large natural disturbances (Johnson et al. 1998; Bergeron et al. 2000), such as wildfires, in the control of the plant succession and the many other structural and functional properties of the boreal forest ecosystem (Foster 1985). Consequently, there is a growing trend to adapt silvicultural practices to conciliate both cost-effective wood production with the integrity of natural ecological dynamics and processes of the boreal forest under a sustainable management policy (Attiwil 1994; CCFM 1995). Although the analogy between sustainable forest management and fire disturbance in boreal ecosystems has some merit (Bergeron et al. 1999), it is crucial to recognize that is also has some limitations, particularly in view of the still limited knowledge of the dynamics of the boreal ecosystems and how it varies within different landscapes.

The boreal forest of Quebec is divided into two bioclimatic domains: the mixed-wood so-called *Abies balsamea-Betula papyfera* domain and the pure coniferous domain also called *Picea mariana*-moss forest (Saucier et al. 1998), the boundary of which is located at ca. 49° 00' N in the north-west of the province. Among the few studies carried out in Quebec directly examining the impacts of forest fires on lake chemistry (e.g. Carignan et al. 2000; Lamontagne et al. 2000; Planas et al. 2000), all were completed in mixed-wood ecoregions, and only two have addressed the long-term effects of fire disturbances (> 5 years) (Enache and Prairie 2000; and in chapter IV). To our knowledge, no study has been conducted on the impact of wildfires on lake biogeochemistry in a coniferous-dominated area. Yet, there is considerable evidence that forest types may modulate the impact of forest fires on nearby waterbodies, either directly or indirectly. Firstly, fires are known to cause different changes in soil chemistry in forest of different types (Dyrness et al. 1989; Paré and Bergeron 1996; Willis et al. 1997; Ollinger et al. 2002). It is also becoming increasingly clear that for the same surficial deposits and time elapsed since the last fire, there are important differences in

succesionnal vegetative trends between mixed-wood and coniferous-dominated forests (De Grandpré et al. 2000; Gauthier et al. 2000). Such vegetation changes can alter the chemistry of surface waters. Studies have shown linkages between canopy chemistry and nutrients and major ions in soil cycling (Paré et al. 1993; Ollinger et al. 2002). In some regions at least, these changes are large enough to be detectable as changes in diatom assemblages (Korsman et al. 1994, Korsman and Segerström 1998).

Because of the terrestrial-aquatic linkage, water body responses reflect the nature and the magnitude of the terrestrial disturbance, in particular as to how it controls the hydrological regime and indirectly the mineral and nutrient inputs to aquatic systems. Research on the effect of fire on water chemistry is important considering that large changes in frequency and intensity of forest fires have been suggested as a consequence of global warming. In this paper, we examine the role of fires in the conifer-dominated catchment on lacustrine changes in pH and nutrients of its receptor lake, Lac à la Pessière. The regional climate and fire frequency records over the last 8000 years surrounding Lac à Pessière (Carcaillet et al. 2001a) provided an ideal opportunity for evaluating the long-term impact of fire in the pure coniferous domain of eastern Canada. Paleoreconstructions of lake chemistry were obtained from diatom analysis while fire history was inferred from charcoal stratigraphy (Carcaillet et al. 2001a). The reconstructed impacts of fires are then compared to other studies carried out in mixed-wood boreal forests (Enache and Prairie 2000; Paterson et al. 1998; Carignan et al. 2000; Philibert et al. submitted).

Study site

Lac à la Pessière (49°30'30"N - 79° 30'00"W) is a small headwater lake located in western Quebec near the boundary with Ontario (Figure 5.1). At an elevation of 280 m a.s.l., its surface covers about four hectares. The lake lies on the flat Clay Belt (Abitibi) and the surficial deposits for the area are mainly composed of glacial till and was formed part of Glacial Lake Ojibway before its drainage into the Tyrell Sea at about 8,470 years ago, when ice retreated, (Veillette 1994, Barber et al. 1999). The ratio of drainage area versus lake area is around 3. Lac à la Pessière is a dimictic closed basin with a maximum depth of 16 meter and a small outflowing brooklet. It develops a strong thermal stratification accompanied with an anoxic hypolimnion during summer (Carcaillet et al. 2001a). Lac à la Pessière is a slightly acidic lake (pH = 6.11), oligotrophic lake (9.5 $\mu g\ l^{-1}$ total phosphorus), and is highly coloured and poorly-buffered (alkalinity = 108 $\mu eq\ l^{-1}$) lake.

Lac à la Pessière is located within the coniferous bioclimatic domain, also called the *Picea mariana*-moss domain, that is characterized by black spruce (*Picea mariana* (Mill)) and to a lesser extent by balsam fir (*Abies balsamea* (Mill)) (Saucier et al. 1998; Gauthier et al. 2000). Mature black spruce-feathermoss forest stands are characterized by a closed coniferous overstorey canopy, a sparse understorey, and a continuous feathermoss carpet covering a thick forest floor (Larsen 1980) that can reach 70 cm of humus. Quaking aspen (*Populus tremuloides* (Michx)) and jack pine (*Pinus banksiana* (Ait. Dumont)) may be abundant at early stages of stand succession. Within the catchment, jack pine forest with understorey of lichens, are dominant on dry sites. Balsam firs regenerate at a few hundreds meters beside the lakeshore in a clear-cut area on mesic soil. Most of the surroundings of Lac à la Pessière are characterized by *Picea mariana* swamp-forest [for further details on the vegetation see Carcaillet et al. (2001a)].

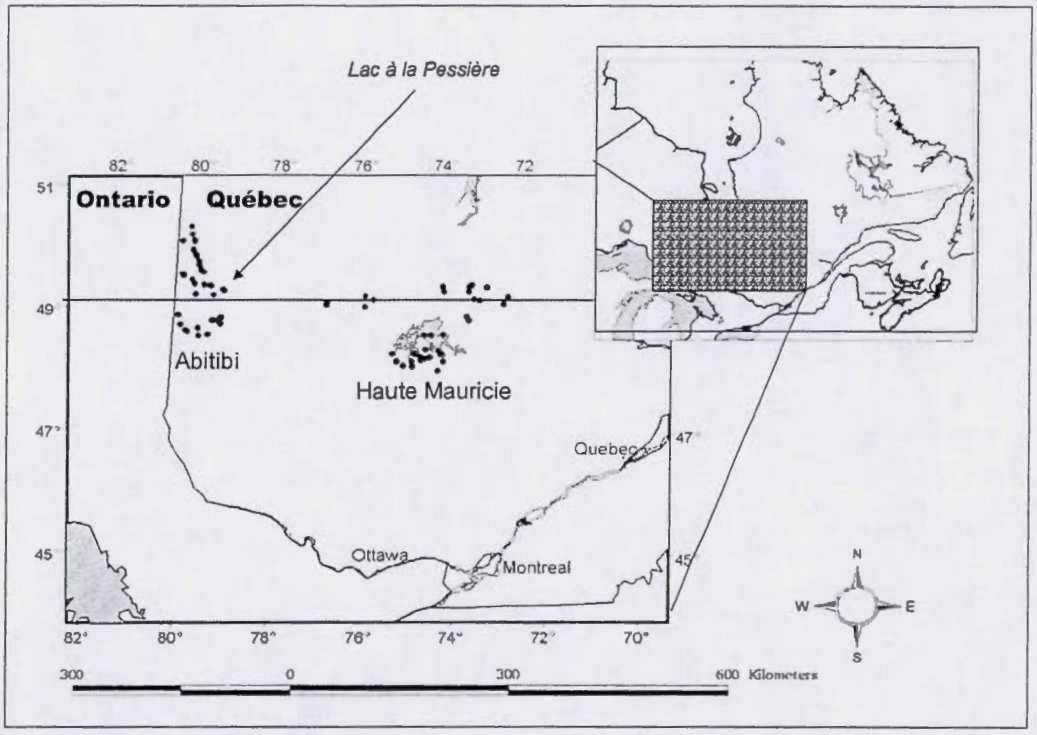

Figure 5.1 Map representing the area of Lac à la Pessière (Abitibi, Quebec) and the 76-training set located in Abitibi and in Haute Mauricie (Quebec).
Lakes sampled are presented by solid circles

Previous calibration set

To reconstruct the effects of forest fire on the biogeochemistry on Lake à la Pessière, we used our 76-lake database to examine the chemical and physical factors controlling lake water quality (Figure 5.1). This database was used to establish the quantitative relationships between the diatom assemblages and the environmental data. For this, a survey was undertaken in the Abitibi-Haute Mauricie areas which cover the continuous boreal forest zone in the two bioclimatic domains: the mixed-wood and the pure coniferous domain. This 76-lake training set was consisted of 41 lakes from Abitibi and 35 from Réservoir Gouin (Haute Mauricie) (Figure 5.1). More details are given in chapter I-Philibert and Prairie (2002a) and Enache and Prairie (2002).

Material and methods

Core sampling and chronology

Whereas a Kajak-Brinkhurst (KB) gravity corer (Glew 1989) was used to collect the top surface sediments (the first centimetre and the next 60 cm), a Mackereth sampler (Mackereth 1948) with a 6-m length was used to retrieve a 5.84 m laminated sediment core from the deepest portion of Lac à la Pessière (i.e. 16 m). The two cores were sliced into one centimeter sections. At each 1 cm section, a 1 cm^3 sample was taken along the longitudinal axis for charcoal pollen and diatom analyses. The KB core overlaps the Mackereth core at 35 cm depth, and stratigraphic correlation has been carried out using pollen assemblages (Carcaillet et al. 2001a, b). The chronology was based on seven calibrated ^{14}C dates from sediment samples and covers the last 8000 calibrated years before present (2000). The deposition time for Lac à la Pessière was about 13 year cm^{-1}. The chronology is detailed in Carcaillet et al. (2001a).

Charcoal analysis

The charcoal analysis protocol is detailed in Carcaillet et al. (2001b), but is briefly summarized here for completeness. Sediment samples were sieved through 150 μm mesh. Sediments were deflocculated in a 3 % $Na_4P_2O_7$ solution for a minimum of two days before a gentle manual water spray was used to aid sieving. The remaining particles were bleached in a Javex water solution (10 %) for a few minutes to clearly distinguish charcoal fragments from dark organic matters. The area of each charcoal fragment was estimated microscopically at 40x magnification using a graticule with 400 pre-calibrated squares in a gridle and was classified into one of ten exponential size-classes: < 0.1197 mm^2; 0.1197-0.2394 mm^2; 0.2394-0.4788 mm^2; 0.4788-1.0773 mm^2; 1.0773-1.9152 mm^2; 1.9152-2.9925 mm^2; 2.9925-5.9850 mm^2; 5.9850-11.9700 mm^2; 11.9700-23.9400 mm^2; > 23.940 mm^2. The total surface area of charcoal in a sample was obtained by summing the mean surface area of each size-class by multipliyng the number of particles in that size-

class over all classes. Charcoal measurements were expressed as charcoal area concentration ($mm^2\ cm^{-2}\ yr^{-1}$).

Fire history reconstruction

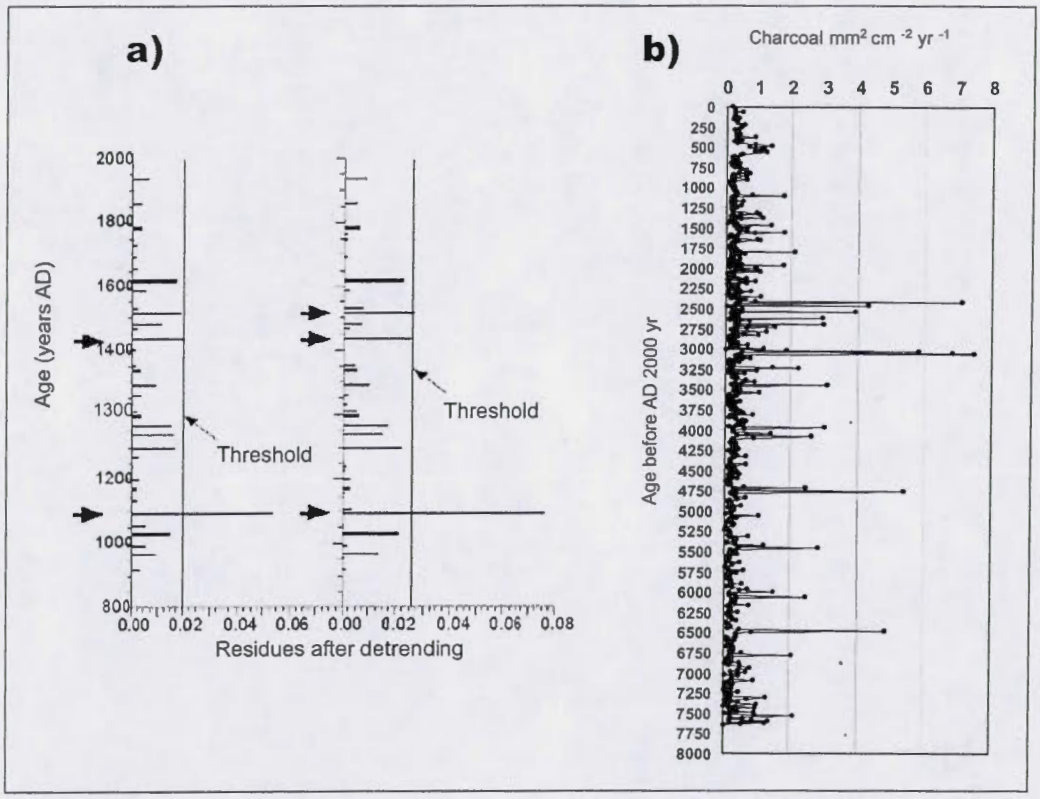

Figure 5.2a) Residues of charcoal accumulation rate (CHAR) since 1200 cal. yr B.P. (AD 800) after detrending the raw CHAR using a window of 3 or 5 observations at left and right, respectively.
Vertical bars correspond to the threshold of 0.021 and 0.026, respectively. The thick black arrows pinpoint the inferred fires.
Figure 5.2 b) Charcoal concentration stratigraphy over the last 8000 cal. yr B.P..

Reconstruction based on awindow of 3 observations		Reconstruction based on a window of 5 observations	
Fire age (AD)	Fire interval (yr)	Fire age (AD)	Fire interval (yr)
2000 (no-fire)	568	2000 (no-fire)	485
1432	539	1515	83
893	210	1432	539
		893	210

Table 5.1: Chronology of fires over the last 1200 years at Lac à la Pessière, inferred from detrended charcoal series resulting from sieved sediments at 150 μm (according to Carcaillet et al. 2001a).

Pollen treatment

Pollen and spores were analysed according to Fægri et al. (1989) with exotic pollen (*Eucalyptus*) added to each sample in order to estimate the pollen concentration. Samples were deflocculated with 10% hot KOH and sieved through a 700 Fm mesh. Carbonates, silicates, and most of the organic matter were removed with 10% HCl, 48% HF and acetolysis, respectively before mounting in glycerine. A minimum of 500 grains was counted per sample. Pollen counts were planned to give a mean time resolution of about 100-120 years over the whole Holocene and samples were taken every 8 cm (4 cm close to the top most cm).The pollen stratigraphy over the last 8000 cal. years is represented in Carcaillet et al. 2001a.

Diatom analysis

Diatom fossil preparation followed techniques outlined in Wilson et al. (1996) using a mixture of HNO_3 and H_2SO_4 (50: 50 by volume). The resulting aliquot from each sample was pipetted onto individual coverslips and mounted on glass slides using Naphrax®, a resine with a mounting high-refractive index. For each sample, a minimum of 500 diatom valves was identified and tallied along random transects at a magnification of 1000x-1600x using a Leica DMR microscope (100x objective, 16x ocular lens) from transects permitting an adequate coverage of the coverslip. Taxonomic identification of diatoms was based on Hustedt (1930-1966), the PIRLA Diatom Iconography (Camburn et al. 1984-1986), Krammer and Lange-Bertalot (1986-1991) and Fallu et al. (2000). A detailed appendix of floristic data characteristics (optima, N2) is available in chapters I and II (Philibert and Prairie 2002a, 2002b). The distinction between planktonic and benthic taxa in our calibration set was established from the litèrature, and according to recommendations from algal taxonomists, included one working in the same region (see chapter II, Philibert and Prairie 2002b for details).

The diatom identification carried out for the present study covers the last 1200 cal. yrs B.P. and was completed at each 1-cm sediment interval, providing a high resolution analysis with a mean resolution of 13 years (average deposition time = 13 yr. cm^{-1}). At least 500 diatom remains were counted and identified at each 1-cm interval. Note that the sediment samples from 57 to 64 cm (946 to 1041 cal. yrs B.P.) recorded poor preservation of diatom remains (a lot of individuals were broken).

Statistical analyses

Predictive models

In this paper, we used two predictive modeling approaches to ascertain and reinforce our past reconstructions of environmental conditions in Lac à la Pessière. The first modeling method has been widely used and consisted in developing Weighted Averaging

Partial Least Squares (WA-PLS) (ter Braak and Juggins 1993) inference functions. In the second approach, we used the paleolimnological application of artificial neuronal networks (ANN) based on the back-propagation algorithm (Rumelhart et al. 1986) recently proposed by Racca et al. (2001). All types of models are based on untransformed species data.

In the first modeling procedure, multivariate statistics were used to identify the environmental factors most strongly correlated with diatom species' distributions. The statistical approach was composed of two main steps of calibration and regression. The first step aimed at assessing the relation between the abundance of modern diatoms (surface sediments) and measured environmental variables. Once the most strongly correlated environmental variables to diatom assemblages were identified, transfer functions were developed in a second step. The transfer function is simply a mathematical formula that estimates environmental variables from diatom species' composition data. Here, WA-PLS transfer functions were used because they take into account the unimodal response of diatoms and use the residuals to diminish bias and to increase performance of models. The theory behind the statistical approaches adopted here are summarized in Birks et al. (1990), Birks (1995) and in Jongman et al. (1995). Even if pH and CO_2 are inextricably related, it has been proposed in a similar study (see chapter I-Philibert and Prairie 2002a) that CO_2 may explain an independent part of the main variance in diatom assemblages. Furthermore, there are some evidences in the literature to suggest that CO_2 may directly affect the ability of diatom taxa to compete in their environment (Kirk 1994). Moreover the reconstruction of CO_2 may be a useful proxy to help determine if a lake is a sink or a source for the surrounding atmosphere.

Significant and predictive WA-PLS models were developed for pH, TP, TN DOC and CO_2 (chapter I-Philibert and Prairie 2002a). The details of the transfer functions are further discussed in chapter I-Philibert and Prairie (2002a). Even though the ANNs technique is also based on <learning> the relationships (seen as examples) between diatom species (inputs) and environmental variables (outputs), non-linearly inter connected neurons or networks are implemented and work in parallel without requiring

any necessary assumption (linear or unimodal) between diatom taxa and variables (Racca et al. 2001). <Learning> is supervised by the back-propagation algorithm (descending gradient algorithm) and consists in the continuous adjustment of the weights of the network connections until optimization is reached (i.e. when the difference between observed and predicted values of the variable to be reconstructed is minimal). More details of the back-propagation procedure and the algorithm are summarized in Racca et al. (2001-Annex).

In a similar study based on the same 76-lake calibration set, (chapter II-Philibert and Prairie (2002b) demonstrated that, by deleting the highest pH tolerant species they obtained the lowest $RMSE_{jackknife}$ of all (0.38 pH units). We thus used the 57 taxa-based set that provided the best WA-PLS model when start with 214 taxa, and we tried out to reconstruct past environmental variables (chapter II-Philibert and Prairie 2002b).

Changes in diatom types

A canonical correspondence analysis (CCA) with forward selection of predictors (pH, TP, TN, DOC, CO_2 and charcoal values) was realized in order to test which predictor variable was able to explain a significant part of the diatom variance using Monte Carlo test permutation ($p < 0.05$). The same was done for all pollen taxa. The CCA was carried out using CANOCO version 3.12 (Jongman et al. 1995; ter Braak, 1988a, 1990b).

Changes in pollen types

Principal component analyses (PCA) were computed to study the changing

vegetation composition and trajectories through time, and to determine the contribution of taxa to these changes. Several PCAs were performed (e.g. for example some included all terrestrial taxa, while others included tree pollen taxa), but the best results, in terms of inertia frequency and eigenvalues, were obtained using the terrestrial taxa whose mean frequency is above 1%. To reduce the weight of the most abundant taxa, the PCA was calculated on the square roots of the pollen frequency for each pollen series. The PCA was performed with PPPBase (Guiot and Goeury 1996).

Evaluation of fit between the modern and fossil diatom assemblages

We used statistical procedures to verify that the calibration set provides suitable analogs for the fossil core samples. The first approach determined if sufficient overlap existed between the calibration model and downcore diatom assemblages in terms of relative abundances from the similarity coefficient squared chord distance (Overpeck et al. 1985). This procedure was implemented using the computer program ANALOG (H.J.B. Birks and J.M. Line, unpublished program). Core samples outside the 95% confidence intervals were considered to have no analogs. The second approach evaluated the degree to which the calibration set provided reliable estimates of reconstructed variables. A canonical correspondence analyses (CCA) constrained to each single explanatory variable was run in order to evaluate the reliability of both models to infer the variables throughout the sediment core. This procedure was completed by calculating the squared residual distance of every core samples (passive data) from the axis 1 in the CCA. Core samples with squared residual distances outside the 95% confidence were deemed as poor analogs for estimating the selected variable (see Birks et al. (1990) for more details).

The relationship between the correspondence analysis (CA) axis scores (an index of main variation in the fossil diatom assemblages) versus the reconstructed variables was undertaken in order to determine which variable drives more the variance in fossil assemblages.

Results

Pollen stratigraphy

The Principal Component Analysis (PCA) applied on pollen frequencies indicated that the vegetation has experienced a subtle change since about 1500 to 1400 cal. yrs B.P. (Figure 5.3). While the inertia and the eigenvalues on the first axis corresponded to 29.4% and to 4.70 respectively, these statistical parameters drop to 17.1% and to 2.74 on the axis 2. The observed change in the vegetation trajectory was observed on the second axis of the PCA (Figure 5.3), where samples primary located on the extreme positive side. Late-Holocene samples showed a location on axis two that is the same as those of the early Holocene samples, characterised by subtle switches in pollen frequencies of jack pine, total herbs, and green alder (*Alnus crispa* (Ait. Purch)) (Figure 5.3). Globally, the vegetation dynamics over the Holocene was very stable at Lac à la Pessière. The pollen diagram (Carcaillet et al. 2001a) was dominated by black spruce and white birch (*Betula papyrifera* (Marsch)) since the afforestation phase (i.e. since 8000 cal. yrs B.P.). The main change corresponded to the rapid decrease in the relative abundance of white cedar (*Thuja occidentalis* (L.)) / Juniper (*Juniperus* (L.)), ca. 4500 cal. yrs B.P. ago. Progressive increases in pollen frequencies of black spruce and of jack pine have occurred since 8000 cal. yrs B.P., while the abundance of white pine (*Pinus strobes* (L.)) decreased (Carcaillet et al. 2001a).

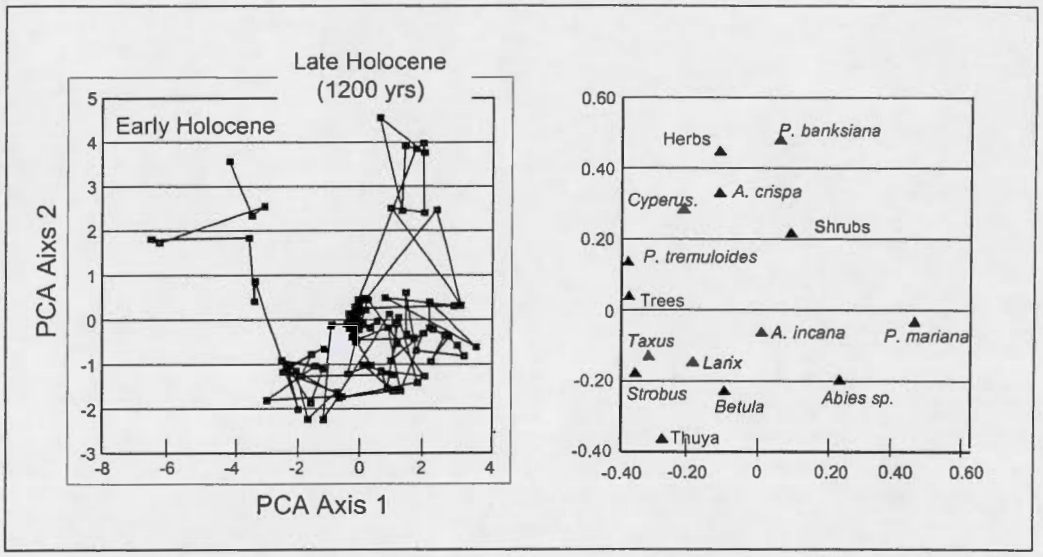

Figure 5.3 Principal Component Analysis applied to pollen data of Lac à la Pessière throughout the Holocene.

Diatom flora stratigraphy

A striking feature of the diatom flora was the low diversity of planktonic taxa, which were mostly composed of *Cyclotella stelligera* (Hustedt) with relative abundances varying between ~ 0 and 40 % throughout the sediment core, and the occurrence of *Tabellaria flocculosa* var. linearis (Koppen) and a few small *T. ventricosa* (Kützing) from depth of 35 cm to the surface over the last ~ 600 years (Figure 5.4). From its great relative frequency at some sediment levels, the main variation in diatom assemblages seemed to be driven by the single species *Cyclotella stelligera.* With the caution that the sediment samples from 57 to 64 cm (946 to 1041 cal. yrs B.P.) exhibited a poor preservation of diatom fossils, *Cyclotella stelligera* generally mirrored the trends exhibited by the benthic taxa *Cymbella hebredica* (Grunow Cleve), *Eunotia faba* (Ehrenberg), *E. rynchocephala* (Krasske) and *Stauroneis anceps* (Ehrenberg) (Figure 5.4). In general, no diatom species seemed to be related the two main fire series excepted for *Cyclotella stelligera* which decreased in relative abundance between 25 and 35 cm depth (451 and 617 cal. yrs B.P.) and between 67 and 70 cm depth (1070 and 1100 cal. yrs B.P.) during the fire event occurring betweeen 451

and 617 cal. yrs B.P., the relative abundance of *Cymbella hebredica*, *Eunotia faba, E. rynchocephala* and *Stauroneis anceps* increased. As a result, it is difficult to ascertain whether the decrease in relative abundance of *Cyclotella stelligera* is attributed to both fire periods or other factors due to its high variability along the sediment core since the last ~ 1200 cal. yrs B.P. The same was concluded for benthic species whose relative frequency varied during fire series.

The diatom flora of the bottom sediment (70-77 cm, between 1120 and 1208 cal. yrs B.P.) was dominated by *Cyclotella stelligera* and, to a lesser extent, by benthic genera such as *Cymbella, Eunotia, Neidium* and *Stauroneis*, especially by *Cymbella hebredica, Eunotia faba*, *E. rhyncocephala*, *Neidium ampliatum* ((Ehrenberg) Krammer) *N. iridis* (Ehrenberg) Kleve) and *Stauroneis anceps* (Figure 3). The latter benthic taxa were relatively dominant from 65 to 43 cm depth (from 1055 to 742 cal. yrs B.P.). From 43 to 35 cm depth (742 and 617 cal. yrs B.P.) *Cyclotella stelligera* increased in relative frequency.

At 35 cm depth (617 cal. yrs B.P.), there was clear shift in diatom assemblages with increases in benthic *Navicula subatomoides* (Hustedt), *P. maior* (I) (Kützing), *Pinnularia mesolepta* ((Ehrenberg) W. Smith), as well as two planktonic taxa *Tabellaria flocculosa* and small *T. ventricosa*. There was also an increase in the relative abundance of *Cymbella hebredica, Eunotia faba*, and, to a lesser extent, *E. rhyncocephala* and *Stauroneis anceps*. The top 22 cm (the last 400 cal. yrs B.P.) were characterized by an almost total dominance of planktonic taxa such as *Cyclotella stelligera* and, to a lesser extent, by *Tabellaria flocculosa* and small *T. ventricosa*. Most of benthic taxa, which were observed throughout the sediment core over the last 1200 cal. yrs B.P., drop to low relative abundances < 5 % or disappeared in the top 22 cm. The more recent diatom assemblages (the top 5 cm depth) were dominated by *Cyclotella stelligera* and marked by a sharp increase in small *T. ventricosa* and, to a lesser extent, by *Tabellaria flocculosa* (Figure 5.4).

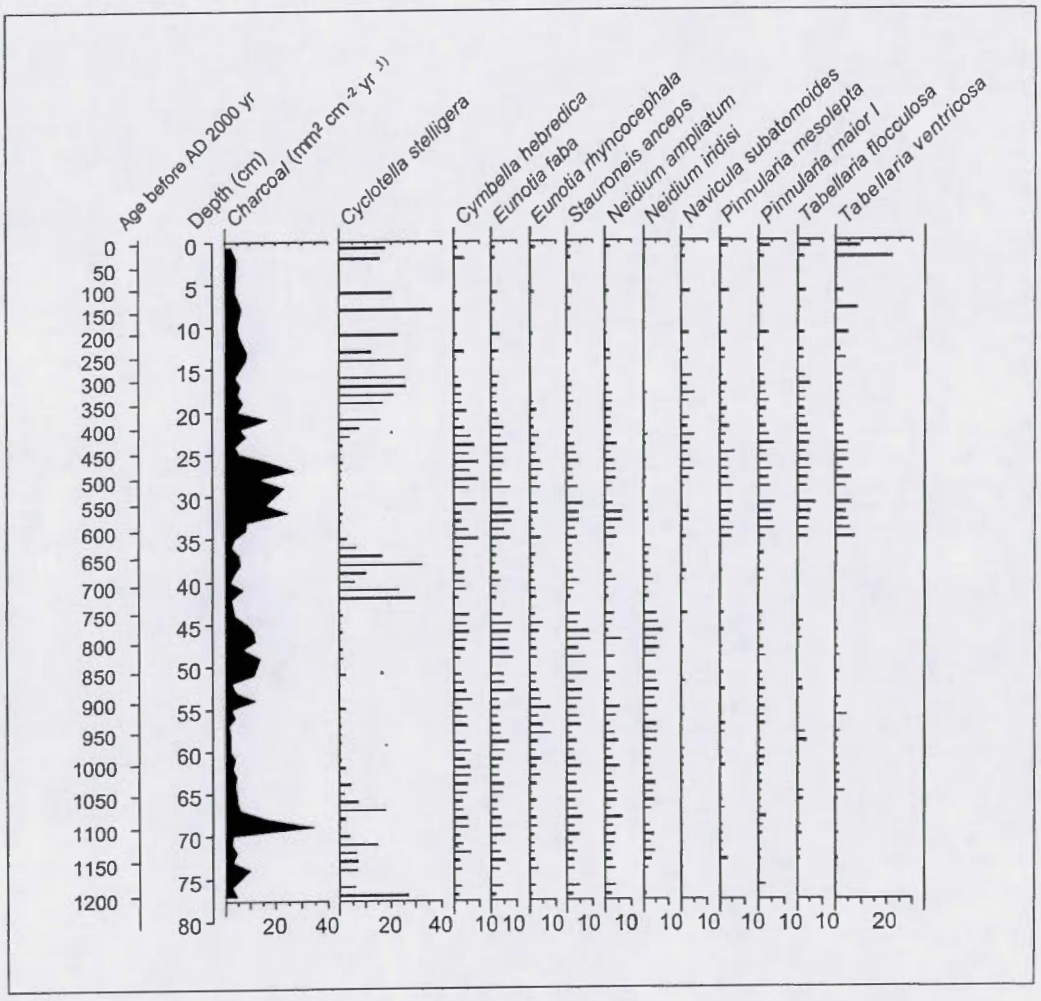

Figure 5.4 Stratigraphic diagram of charcoal concentration and of main diatom taxa in Lac à la Pessière over the last 1200 cal. yr B.p.

Evaluation of predictive models

A total of 214 diatom taxa were identified from the surface sediments in our calibration set. Fifty-five taxa were collected throughout the sediment samples of Lac à la Pessière.

In the reduced 57 taxa-based calibration set (chapter II-Philibert and Prairie 2002b), only 50 % of core samples showed a good correspondence between modern diatom and fossil diatom assemblages. The lack of good analogs prevented the use of the pH WA-PLS model from chapter II-Philibert and Prairie (2002b). We therefore used the significant and reliable WA-PLS models from chapter I-Philibert and Prairie (2002a) utilizying the same 76-lake calibration set, but using all 214 diatom taxa. The ANN pH and CO_2 models were significant in term of jackknife procedure (pH: $r^2_{jackknife} = 0.64$, $RMSE_{jackknife} = 0.44$, ln CO_2: $r^2_{jackknife} = 0.64$, $RMSE_{jackknife} = 0.63$) (Figure 5.5). There was a good correspondence between the actual measured and estimated values at the sediment surface for all variables, with each measured value falling within the 95 % confidence interval in the WA-PLS or in the ANN model. This supported our belief that our models were reliable. The very good correlation between reconstructed ANN pH and WA–PLS pH values ($R^2 = 0.83$, $p < 0.001$) and between ANN CO_2 and WA-PLS CO_2 values ($R^2 = 0.92$, $p < 0.001$) throughout the sediment core supported the reliability of our WA-PLS and ANN models for reconstructing these variables.

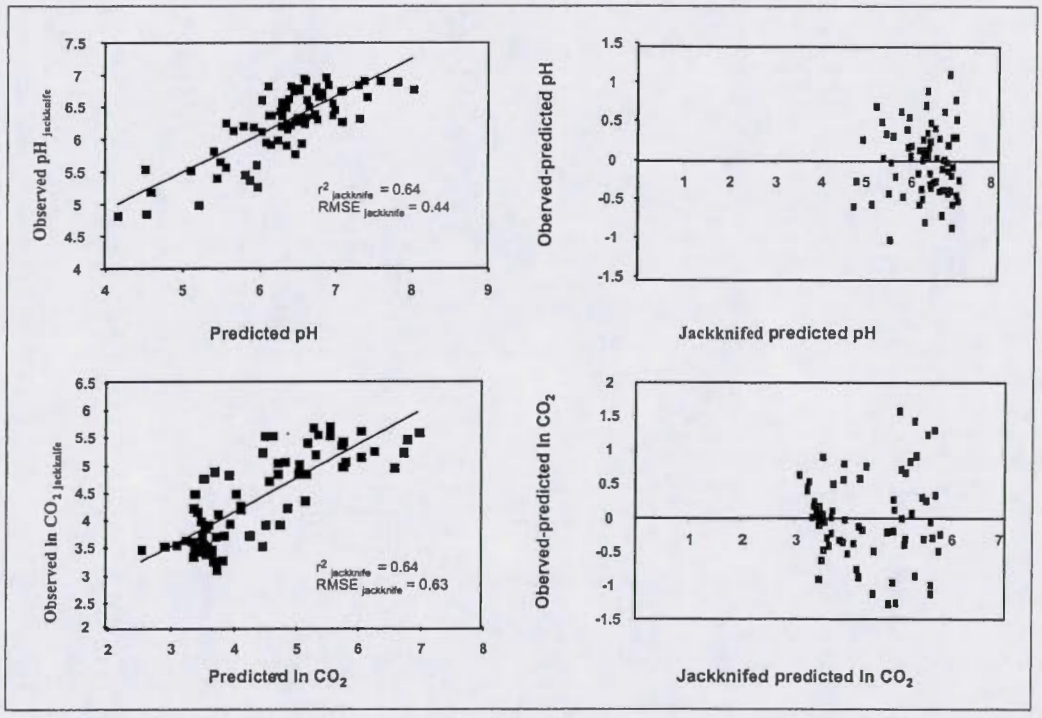

Figure 5.5 Plot of observed pH (and ln CO_2) values for the 76-lake modern calibration set against jackknifed predicted pH (and ln CO_2) values are shown in (a). The plot of observed minus predicted values against predicted values were also represented in (b).
The jackknife resampling procedure was based on leave-one-out test on each lake of the calibration set.

Evaluation of fit for predictive models between modern calibration set and sediment core

The computer program ANALOG identified strong and reliable analogs between the 76 lake-modern calibration set and downcore species assemblages in terms of relative abundance throughout the sediment core. The modern calibration set contained 95 % of the fossil taxa. In terms of species, 49 on the 55 core diatom fossils were represented in the modern calibration set. All taxa even rare taxa that belonged to the modern calibration set were taken account into the predictive models. Likewise, most of the dominant species in the core stratigraphy have high Hill's N2 values (e.g., 1 to 21.8;

mean = 7.1) in the calibration set, suggesting that their ecology was well circumscribed and our diatom-based reconstructions reliable (for more details on ecological characteristics on these species, see chapter I-Philibert and Prairie (2002a).

The analyses of squared residual structures in the CCAs constrained to each environmental reconstructed variable for pH, TP, TN, DOC and CO_2 in WA-PLS models and pH and CO_2 in ANN models demonstrated that the reliability for each reconstructed variable was strong enough along the core because, for each reconstructed variable, at least 78 % of the core residuals fell within the 95% confidence intervals in the calibration set residuals. The sample cores that presented the worst analogs in terms of reliable reconstruction were the same for WA-PLS and ANN, and were located at 7, 13, 21, 36-43, 44-50, 55 and 71 cm sediment depths (Figure 5.6). Although the analogs in terms of species assemblages were adequat, reconstructed variables for these samples are less reliable. A partial CCA (pCCA) taking into account charcoal as the sole predictor was not significant in terms of all diatom variance change. When running a CCA with forward selection on the pollen taxa, green alder (*Alnus crispa*) was the only variable explaining a significant part of the variance in the fossil diatom composition.

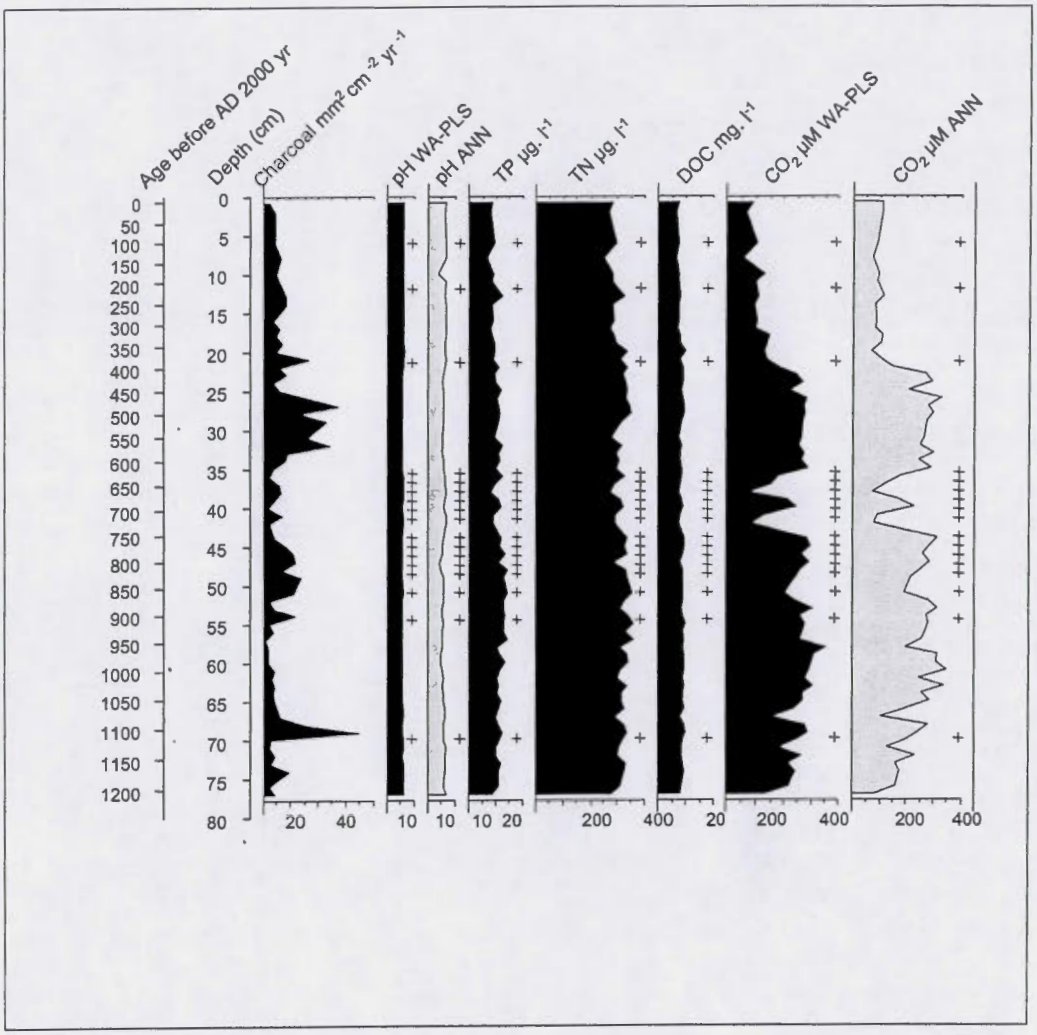

Figure 5.6 Stratigraphic diagram of charcoal concentration and of the reconstructed variables from diatom remains by implemented WA-PLS and ANN models in the sediment core of Lake à la Pessières over the last 1200 cal. years.
Cross (+) indicated less good analogs estimated values from WA-PLS and ANN models.

Reconstructed environmental variables

The reconstructed pH and CO_2 variables from WA-PLS and ANN techniques were very similar, both in trends and absolute values (Figure 5.6). This similarity reinforced the reconstruction of both variables. In Lac à la Pessière, no diatom-inferred variables appeared correlated with fire events. Diatom-inferred values during fires (i.e. between 25 and 35 cm (451 and 617 cal. yrs B.P.) and between 67 and 69 cm (1070 and 1100 cal yrs. B.P.) were not significantly different from pre-fire and post-fire levels, when considering the pre-3 cm and post-3 cm fire levels excepted for the variable CO_2 between 25 and 35 cm. In addition, no major trend was seen in the diatom-inferred pH, TP, TN and DOC values throughout the sediment core over the last ~ 1200 cal. yrs B.P., because they did not represent the main direction of variation in the taxa. The reconstructed CO_2 values explained up to 81 % of the main direction of variation in the fossil taxa along the sediment core from the CA axis 1 scores.

Surprisingly, the reconstructed dissolved CO_2 concentrations showed a decrease over the last 400 cal. yrs B.P. (Figure 5.6). This decrease coincided first with an increase in *Cyclotella stelligera* that have CO_2 optima value of 64 µM. There is This decrease also coincided with the disappearance of mainly benthic taxa whose optima for CO_2 are quite elevated in the modern calibration set (*Cymbella hebredica*, *Eunotia faba*, *E. rhyncocephala* and *Neidium ampliatum*) have CO_2 optima values of 586, 291, 254 and 483 µM, respectively.

Discussion

The most important result of our study is the apparent lack of forest fire impact on diatom communities and, by extension, on reconstructed lake chemistry on the Lac à la Pessière catchment area. The only significant deviation from this generalization was especially for the decrease in the relative abundance of *Cyclotella stelligera* but it is ascertain to suggest a real relationship. If fire really affects some species, it does not appear to be

the only factor impacting diatom assemblages (particularly *Cyclotella stelligera*), given that the interval between ~ 750 and 1000 cal. yrs B.P. with no fires does not have high relative abundance of *Cyclotella stelligera.* As well, other changes in the diatom stratigraphy, as outlined in this manuscript, such as decreases in several benthics around 400 cal. yrs B.P. and increases in other benthics and *Tabellaria* sp. around 600 cal. yrs B.P., do not appear to be strictly coincident with fire. Even when supported by reliable analogs, no significant change was observed in inferred lake water chemistry (nutrients, pH or DOC) during fire events, except for diatom-inferred CO_2 values between 25 and 35 cm (Figure 6). The CO_2 values are highly correlated to the relative frequency of *Cyclotella stelligera* along the core ($R^2 = 0.86$, $p < 0.0001$) and because this latter species seems to drive at itself the all reconstruction, CO_2 values strongly depend on it. Even if we argue that the appreciation of the optima of *Cyclotella stelligera* may present some uncertainties, the error is conservative and the same error was reported along the entire sediment core, therefore all variations observed in the reconstructions remain reliable.

There was a sharp decline in CO_2 values coincident with a sharp increase in *Cyclotella stelligera* over the last ~ 400 cal. yrs B.P. A similar decline in CO_2 has also been observed in L. Francis (Philibert thesis). While the exact nature of this decline remains unclear, it appears to be a regional phenomenon unrelated to fires. However, this decreased CO_2 result is tentative, because diatom-inferred CO_2 concentrations exhibited a large variability along the sediment core portion we studied. Several hypotheses may be considered even if not tested. Once the Proglacial Ojibway Lake drained to the Tyrell Sea ~ 8740 years ago, clay surface deposits rich in carbonates were settled in the Abitibi region. Litle by little, organic acids from vegetal detritus may have acidified carbonates in the upper layer of soils and thus provided a possible production of CO_2 in the soil water and then into the groundwater network. Along centuries, carbonates have been progressively acidified and eliminated from upper horizons. The remaining carbonates lay on horizons C at a deeper depth, which are associated with a lower temperature and where chemical reactions are the slightest. This could explain a lower production of CO_2 from the catchment into the lake. With an ageing of soils, organics acids originated from

the vegetation may have buffered from other reactions such as cationic exchanges. Another possibility will be a deccrease in oxygen concentration in the soil waters involving a decrease in the aerobic decomposition of organic matter and therefore a decrease in the production of CO_2. Also a change in the soil fauna may have drive changes in the decomposition of organic matter within the soils.

If applicable to other lakes of the same region, our results indicate that the consequences of forest fires on lakes within conifer-dominated areas are probably small, either in magnitude, in temporal extent, or both. We suggest that this is likely the result of the bog-like nature of the forest's understorey, a feature characteristic of this region. As a consequence of cooler climate and excess moisture in such coniferous ecoregions, as well as the resistance of lignified stands and the strong acidic forest layer, decomposition rates are slow and organic layers accumulate (Heinselman 1981; Moore 1981; Økland 2000). This excess moisture and the thick humus of the soil may be incompletely removed by fire and therefore likely limits the mobilization of nutrients and major ions during fire events (Foster 1985, Ollinger 2002).

A second possible explanation for the lack of effect of fires on lakes in coniferous forests may be more indirect, through the influence of fire on vegetation composition. Indeed, black spruce and jack pine establish rapidly by seed release from serotinous cones and, following fires, even-aged stages are often coupled with the resurgence of understorey vegetation, leading to very little floristic variation (Vierek and Schandelmeier 1980; Foster 1985). According to a study of Gauthier et al. (2000) in Quebec, the post-fire succession is more diverse in the mixed-wood ecoregion than in the coniferous domain, where large areas occupied by organic surficial material remained favorable to black spruce dominance (Sims et al. 1990). Indeed, the Holocene pollen series from lakes located in black spruce dominated forests (Garralla and Gajewski 1992; present study) provide strong evidence for a remarkable stability and uniformity of the surrounding vegetation over the last ~ 8000 cal. yrs B.P. Consequently, we suggest that forest fires in such stable coniferous-dominated catchment may have lesser or a shorter impact on the biogeochemistry of lakes than similar fires in mixed-wood catchments (Enache and

Praire 2000) because of the stability of the forest composition after fires.

The present results diverge from those obtained in mixedwood forests either through direct post-fire measurements (Carignan et al. 2000) or through similar paleolimnological studies of Lac Francis very closed geographically to Lac à la Pessière (Enache and Prairie 2002) where fires induced a detectable change in inferred phosphorus concentrations. A related but possibly confounding factor is the average fire interval over the last 1000 cal. yrs B.P. that is shorter at L. Francis (203 ±83 years) than it is at L. à la Pessière (> 400 years). Consequently, the lower organic matter accumulation in the catchment of Lac Francis may have facilitated the removal of organic matter and the exposure of mineral soil, thereby promoting the drainage of materials into the lake.

Other explanations are also possible. Carignan et al. (2000) hypothesized that the greater the ratio of the burn area divided by either the volume of the lake or the lake's surface area, the greater the biogeochemical impact. The lack of response in Lac à la Pessière may be attributable to the lower drainage ratio (about 3) as compared to L. Francis (greater than 7.5). Similar studies on other lakes of the conifer-dominated region, but with larger drainage ratios, will be necessary to test the generality of this trend.

Implications

The present study shows that diatom assemblages are unlikely dependent on fire regime on a decadal or secular scale. However more studies are needed to confirm or to infirm this status. No trends associated with the scale-dependent climatic forcing of the last millennium have been observed. These data suggest that lacustrine biogeochemical dynamics are controlled by longer time scale processes such as those triggered by millennial scale climatic changes, or by secular scale climatic processes with magnitudes larger than those that occurred during the last ~ 1000 years inferred from multi-proxies reconstruction (Luckman et al. 1997; Overpeck et al. 1997; Briffa et al. 2001.; Jones et al. 2001).

In western Quebec, global warming is predicted to lengthen the fire cycle (Bergeron

and Archambault 1993; Flannigan et al. 2001) and to decrease the likelihood of drought occurrence during the growing season (Carcaillet and Richard 2000). Combined with a warmer but wetter climate, this may allow more organic matter to accumulate and favor the formation of peat land and as well as the dominance of old growth forests of *Picea mariana* regenerating by layering, such as around Lac à la Pessière. Factors such as pre-disturbance stand composition, stand moisture and nutrient regime, and time since the last disturbance have all been recognized as exerting a greater influence on post-disturbance stand composition than disturbance type itself (Noble et al. 1977; Carleton and MacLellan, 1994; Ehnes 1998). Regardless of the accuracy of the global warming predictions, we stress the need for more studies exploring the long-term relationships between terrestrial and aquatic processes within boreal forest. This is particularly important in closed-crown coniferous forests, where we have little information on how forest composition may modulate the effects of forest fires on lakes.

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Chapitre VI

Impact of mid-20th century logging practices on lake biogeochemistry in Haute Mauricie (Quebec, Canada) as inferred from diatom remains: implications for sustainable management in the boreal forest.

En préparation

Aline Philibert and Yves T. Prairie

Résumé

Il existe un besoin croissant de développer des outils capables d'évaluer les impacts des coupes forestières par rapport aux impacts des perturbations naturelles afin de fournir à long terme une production de bois rentable et une productivité soutenue. L'impact des coupes partielles entre 1935 et 1960 sur la biogéochimie des lacs a été examiné dans trois lacs du Bouclier Précambrien en Haute Mauricie (Québec). A cet endroit 60 à 80 % du basin de drainage a été progressivement coupé sur 5 à 10 ans et ceci pendant les périodes hivernales. Une étude paléolimnologique a été mise en œuvre pour reconstruire les changements des conditions environnementales après coupes et ceci à partir des restes de diatomées dans les sédiments lacustres. Les variables étudiées étaient le pH, le phosphore total (PT), l'azote total (NT) et le carbone organique dissous (COD). Une comparaison de la composition diatomique et implicitement des variables reconstruites a été faite avant et après coupe. Un changement rapide et de faible amplitude dans la composition diatomique fut observé dans un des lacs d'étude (moins de 10 ans) et a révélé une petite augmentation en COD. Cependant aucune variation n'a été observée dans les autres lacs. Ces résultats suggèrent que, si les coupes partielles induisent effectivement un changement dans la chimie des lacs, l'amplitude et la durée de l'impact sont trop faibles pour être détectables à partir des assemblages de diatomées. Nous expliquons ces résultats par la période (hiver) et le type de coupes effectuées (anciennes technologies et coupes partielles) qui empêchent ou tout du moins réduisent toute perturbation tant au niveau du sol qu'au niveau de la régénération de la végétation pré-établie.

Abstract

There is an increased need for developing tools capable of evaluating the impacts of logging practices relative to those of comparable natural disturbances in order to provide cost effective wood production with long-term sustainable productivity. The impact of partial forest cutting (1935-1960) on lake biogeochemistry was examined in three lakes on the Canadian Precambrian Shield in Haute Mauricie (Quebec) where 60-80 % of the catchment area have been progressively cut during the winter over periods ranging from 5 to 10 years. A paleolimnological study was carried out using diatom remains (class: *Bacillariophyceae*) to reconstruct changes in environmental variables of limnological interest (pH, total phosphorus (TP), total nitrogen (TN) and dissolved organic carbon (DOC)) following timber harvesting. We compared diatom composition and related reconstructed variables of limnological interest before and after logging events. In one lake, a small and short-lived (less than 10 years) change in the diatom assemblage inferred a small increase in DOC concentrations. However, two other lakes did not show any variation in diatom assemblage. In no case were changes in total diatom abundance observed. These results suggest that, if the partial logging induced a change in lake chemistry, the magnitude or the duration of the change was too small to be detectable from diatom assemblages. We explain such results by considering that the old partial logging techniques may have prevented any soil and pre-established vegetative regeneration disturbances, especially when conducted during the winter.

Introduction

The boreal forest in increasingly viewed as an important ecosystem for wildlife, recreation and biodiversity conservation (Kimmins 1995; Lieffers et al. 1996). This awareness has resulted in a vision of sustainable ecosystem management that integrates both natural and human disturbances. Disturbances such as wildfires and insect outbreaks are frequent and part of the natural dynamic of the boreal ecosystem (Bergeron et al. 1999). This fact leads to the following conception: an organism- and by extension an ecosystem - capable of withstanding large natural perturbations (e.g. wildfires, insect epidemics, and storms) is probably "adapted" to withstand human perturbations of comparable magnitude and frequency (Bergeron et al. 1999). One avenue being given attention is the establishment of tools capable of estimating the impacts of logging practices relative to those of comparable natural disturbances. The main goal being to adapt silvicultural interventions to reconcile cost-effective wood production with biodiversity maintenance and long-term productivity under sustainable management (Mann et al. 1988; Kimmins 1995; Bergeron and Harvey 1997). Forest harvesting (clearcutting) in a watershed can alter external nutrient inputs and runoff (Cooke and Prepas 1998; Lamontagne et al. 2000; Prepas et al. 2001) thereby changing lakewater quality. Carignan et al. (2000) developed predictive models of lakewater quality based on the ratio of clearcut surface area to the area or volume of the receptor lake; the greater the drainage ratio, the greater the impact. Logging practices modify lake hydrochemistry and thus the structure and function of the organisms living in the surrounding lakes in complex ways. While a few studies carried out in Haute Mauricie (Réservoir Gouin) have clearly shown an impact of clearcutting on lakewater chemistry (Carignan et al. 2000, Lamontagne et al. 2000; Planas et al. 2000), the temporal extent of these changes are still largely unknown and paleo-reconstructions in other areas have shown that these impacts are not always easily distinguished from background environmental variations (Paterson et al. 1998; Laird and Cumming 2001; Laird et al. 2001). In order to fill some of these gaps, a paleolimnological study was undertaken in

the same area to determine whether the magnitude of impacts of timber harvesting on nutrient losses and associated algal biomass increases proposed by Carignan et al. (2000), Planas et al. (2000) and Prepas et al. (2001), were observed in lakes whose catchment was partially but continuously harvested over a few years (5 to 10 years). The period under study (1940-1960) coincided with the onset of mechanized forest harvesting in Haute Mauricie (Réservoir Gouin) and therefore allows us to compare the impacts of these historical logging practices relative to the still pervasive clearcutting methods. We used records of diatom remains from three lakes, Lac sans nom (C1), Lac Arthur (C2) and Lac Rouillard (C3) surrounding the Réservoir Gouin in Haute Mauricie. Diatom analysis was used as the single-celled algae, are the most widely used and sensitive indicators of past changes in lake environment (Stoermer and Smol 1999).

Study sites

Due to the complexity of logging practices impacts on the hydrogeochemistry and consequently the structure and function of organisms in lakes, a clear answer from the paleolimnological record may be difficult to obtain. However this complexity can be addressed through analysis of sediment cores from multiples lakes in the same area. The use of reference lakes can be replaced by the long-term study, in each lake of natural variability prior to forest harvesting. Furthermore, even if comparisons with reference lakes are used, some uncertainties will always remain, as it is nearly impossible to have control lakes of exactly the same lake/catchment characteristics (percent of logged area, geomorphology, vegetation, physical and chemical characteristics). We used records of diatom remains from three lakes, Lac sans nom (C1), L. Arthur (C2) and L. Rouillard (C3) surrounding the Réservoir Gouin in Haute Mauricie (48°05' N-49°00' N, 73°15'-74°00' W) (Figure 6.1). Site selection was determined using logging company records (Cartons Saint Laurent, La Tuque) of the harvesting period, the type (partial) and percentage of logging, the proximity of lakes, the surface of the territory under study (< 100 km^2), the accessibility to the lakes, and the ratio of the drainage area to lake area (> 5). These lakes were not affected by prior logging disturbances (logging company

pers.comm.). The main characteristics of the three lakes are summarized in Table 6.1. The lakes are found on the Precambrian Shield, composed of metamorphic and crystalline rocks (graniodorites, gneiss). A till of varying thickness covers surrounding uplands. The till veneer is thin on upland slopes while thicker till deposits are located in thalwegs and in areas with low slope. Climate is subpolar to subhumid continental. The region lies in the balsam fir-white birch forest climatic biome and is dominated by balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyfera*) (De Grandpré et al.1996; Ordre des ingénieurs du Québec 1996).

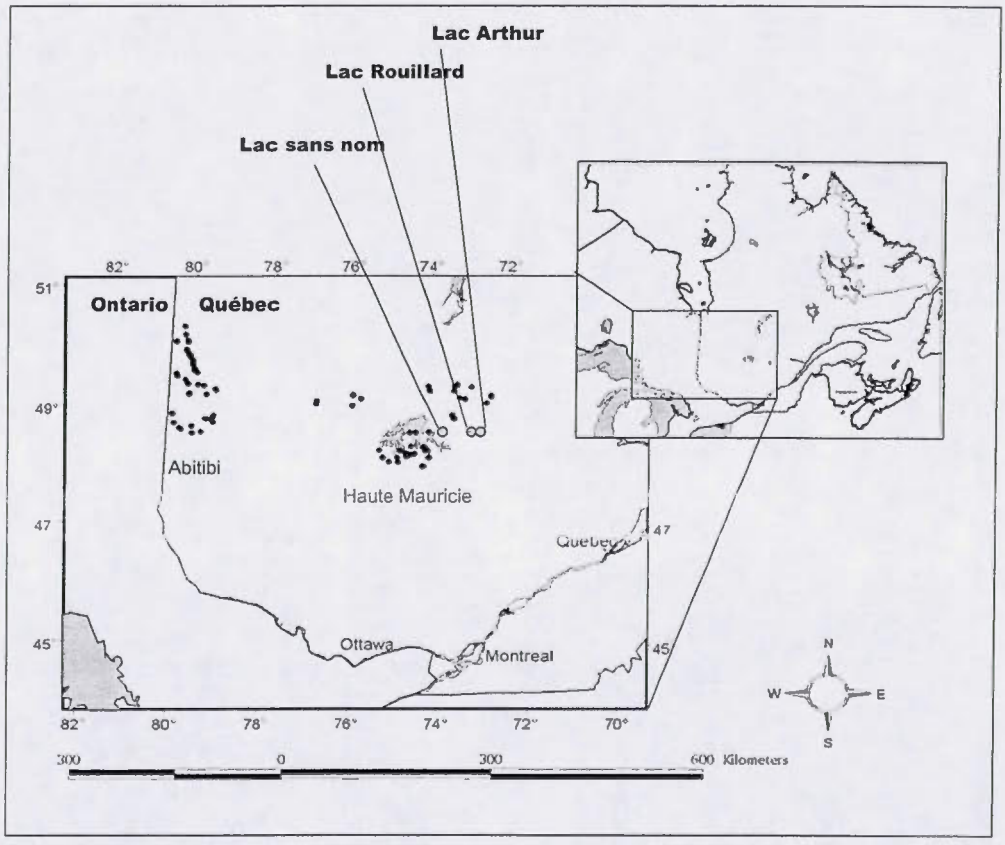

Figure 6.1 Map of the training set in Abitibi-Haute Mauricie (Quebec, Canada) and the location of Lac sans nom, L. Arthur and L. Rouillard.

Previous calibration

Surface sediments representing the last few years of deposit, were collected from our 76-lake modern calibration set in order to establish quantitative relationships between diatom assemblages and chemical variables and we thus developed predictive models in chapter I (Philibert and Prairie 2002a). Our calibration set consisted of 41 lakes located in Abitibi while 35 of them were located in the area presently under study. All lakes are located on the Precambrian Canadian Shield. The Haute Mauricie area lies on glacial till, whereas surficial deposits are mainly composed of glacio-lacustrine fine grains, tills (Robitaille and Saucier 1998). In contrast, Abitibi is part of the Clay Belt region of Quebec dominated by clay deposits. The Haute Mauricie is located in the domain of western balsam fir-white birch forest (76%) and overlaps the black spruce forest-feathermoss area (2%). This ecoregion is dominated by balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), black spruce (*Picea mariana*), white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) (De Grandpré et al. 1996). In southern Abitibi balsam fir, white birch and white spruce (*Picea glauca*) are dominant on mesic sites, whereas black spruce, white cedar (*Thuya occidentalis*), eastern larch (*Larix laricina*) associated with black ash (*Fraxinus nigra*) and American helm (*Ulmus Americana*) are dominant on bogs. In northern Abitibi the forest is dominated by spruce species and belongs to the *Picea mariana*-moss domain (more details are given in chapter I- Philibert and Prairie 2002a).

Logging history in Haute Mauricie

In the Haute Mauricie, as in most regions in Quebec, commercial forestry activities started with the development of the transcontinental railway around 1912. This development was accompanied little by little by the establishment of numerous pulp and paper companies as well as an increase in demand in the coniferous wood market, especially spruce and balsam fir (Parks Canada). Quickly, forests were exploited and harvested, making wood commercialization replace wildfires as the main source of disturbance in the boreal forest ecosystem. Whereas the large scale harvesting started in

the south part of the Réservoir Gouin around 1940, the boom of harvesting in northern areas took place at the end of the 70's (Lessieur 2000). While axes and saws were still common until the end of the 1950's, they were later replaced by chain saws, wheel skidders and hydraulic loaders (heavy machinery)s. Horses were replaced by tracked hauling machines. Until the end of 1960's most timber harvestings were partial logging and were conducted during the winter period in Haute Mauricie (logging company, pers. comm.). Some settlers were hired by lumbing companies and stayed in camps over the winter, while others stayed on their lands to cut wood and sell it to the paper companies.

Material and methods

Sediment analyses

Polycarbonate tubes (diameter 7.5 cm) from an Ekman mechanical grab (30 cm X 30cm X 60 cm) were used to sample sediments cores at the deepest point of each basin. Lead-210 dating analyses were performed for each lake on the same sediment core that was used for the diatom analyses (Oldfield and Appleby 1984; Appleby et al. 1986). ^{210}Pb measurements were performed in the laboratory of Richard Carignan (Université of Montréal). Plots of accumulated weight of ^{210}Pb (constant rate of supply (CRS) technique) versus age summarizes the sedimentation rates of the study lakes over the 20th century (Figure 6.2). The core was sliced into one-centimeter sections along the longitudinal Axis of the core. One centimeter sample intervals represents an average time frame of 10, 8, and 5 years for Lac sans nom, L. Arthur and L. Rouillard, respectively. These time frames correspond to relatively high sedimentation rates for the region, when compared with other studies (Enache and Prairie 2000; Carcaillet et al. 2001a, b).

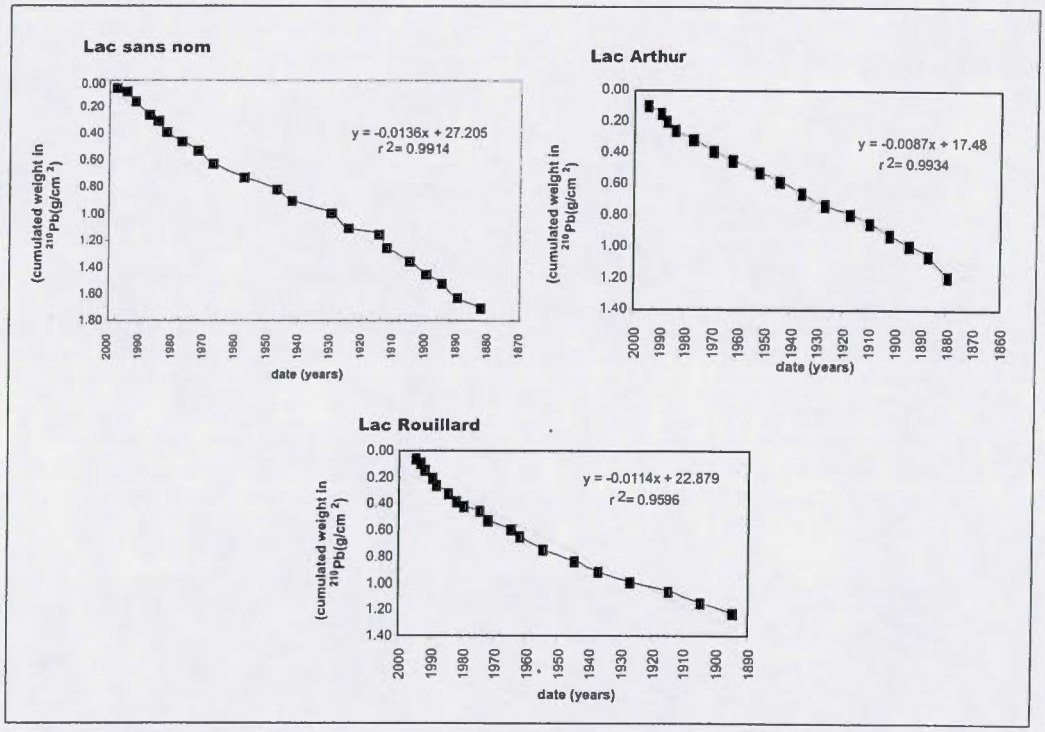

Figure 6.2 Plots of accumulated weight of ^{210}Pb (CRS) versus datation summarized sedimentation rates between study lakes over the 20th century.
The plots indicated a likely constant rate of sedimentation for each sediment core in Lac sans nom, Lac Arthur and Lac Rouillard respectively.

Diatom analysis

The analysis of surface sediment diatoms and fossil diatoms was done using standard paleolimnological techniques. A sub-sample of wet sediment (less than 0.5 g) was boiled in either H_2O_2 (Battarbee, 1973, 1986) or in a 50:50 mixture of HNO_3: H_2SO_4 (Wilson et al. 1996) in order to digest organic material. After setlle for 24h, 15 mL of acid residue were replaced with distilled water. This operation was repeated 6 times. The supernatant was removed and the siliceous material (pellet) was resuspended in distilled water and evaporated onto coverslips. Slides were mounted with Naphrax resin. Taxonomy and nomenclature were based on Hustedt (1930-1966), Krammer and Lange-Bertalot (1986-

1991), the PIRLA Diatom Iconography (Camburn et al. 1984-1986), and Fallu et al. (2000). We evaluated the total abundance of valves of diatom per gram of oven dried sediment in each interval from a standardized solution of *Eucalyptus globulus*. A detailed appendix of floristic data characteristics (optimas) is available in chapter I-Philibert and Prairie (2002a). For each core sample, a minimum of 500 diatom valves was counted and identified along random transects at a magnification of 1000x-1600x using a Leica DMR microscope.

Numerical analysis

Correlations between diatom assemblages and limnological variables were measured by multivariate statistical techniques and were used to derive transfer functions (or predictive models) for the reconstruction of variables from fossil remains. The statistical approach is composed of two main steps, calibration and regression. The first one aims at assessing the relation between the relative abundance of modern diatoms and actual environmental variables. Once the most strongly correlated environmental variables to diatom assemblages are identified, predictive models can be developed (regression step). The models we used were based on the weighted averaging partial least squares (WA-PLS) technique and took into account both the unimodal response of diatoms along environmental gradients, and the information contained in the residuals, thereby diminishing bias (ter Braak and Juggins 1993). The predictive ability of the calibration models was assessed using the apparent coefficient of determination (r^2) between measured and the diatom-inferred values, and the apparent root mean squared error (RMSE). We also used estimates based on jackknife resampling, $r^2_{jackknife}$ and $RMSE_{jackknife}$, because they represent more realistic measures of the predictive power than the apparent r^2 or RMSE. The analyses were carried out using a SAS/IML implementation of the WA-PLS algorithm (Prairie, unpublished program). The details of the transfer functions are reported in chapter I-Philibert and Prairie (2002a). Significant and predictive WA-PLS models were developed for pH, total phosphorus (TP), total nitrogen (TN), and dissolved organic carbon (DOC).

We used statistical procedures to examine whether the modern calibration set provided suitable analogs for the fossil core samples. The first approach ensured that sufficient overlap existed between the relative abundance of diatom taxa found in the sediment core and the assemblages of the modern calibration model. This was implemented by the computer program ANALOG (H.J.B. Birks and J.M. Line, unpublished program). The similarity coefficient we chose was the squared chord distance (Overpeck et al. 1985). Confidence intervals were based on the mean minimum DC (chord distance) distance within the modern training set. Core samples above 95% confidence intervals were considered to have no analogs. The second approach evaluated the degree to which the calibration set provided reliable estimates of reconstructed variables. We performed separate canonical correspondence analyses (CCA) constrained to one single explanatory variable in order to evaluate the reliability of WA-PLS models to infer each environmental variable throughout the sediment core. This was completed by calculating the squared residual distance of every core samples (passive data) from the Axis 1 in the CCA for each single predictor variable. Core samples with squared residual distances outside the 95% confidence limit were deemed as very poor analogs for estimating the selected variable. More details are given in Birks et al. (1990) and these procedures have been used in other similar paleoecological analyses (Laird et al. 1998; Laing et al. 1999).

We assessed shifts in diatom composition during the three periods (pre-logging, logging and post- logging) using a multi-response permutation procedure (MRPP) based on relative abundance. Pre and post logging corresponded to the 3 cm intervals respectively below and above the sediment core sections corresponding to the period of logging. MRPP is a non-parametric procedure for testing the null hypothesis of no difference in diatom composition between pre-harvest (and post- logging) levels and in the fire level. The difference between groups was assessed by Euclidean distance. A student T-test statistic (using $p < 0.05$) described the separation between two groups based on the within-group and inter-group variance. This procedure was implemented by the computer program PC-ORD version 2.0 (MJM Software Design 1995). The

Indicator Species Analysis was used to calculate the contribution of each species to the similarity or dissimilarity between pre-, post-logging and during the logging period (1935-1940), computed in the MRRP test. A very common goal in community analysis is to detect and describe the value of different species as indicators of environmental conditions. If pre- logging, post- logging and logging periods are conceptualized as groups of sample units, then Dufrene and Legendre's (1997) method of calculating species indicator values provides a simple, intuitive solution. The method combines information on the species' relative abundance in a particular group and the faithfulness of occurrence of a species in a particular group. It produces indicator values for each species in each group based on the degree to which they discriminate among groups. These are tested for statistical significance using a Monte Carlo technique for which the alpha value was set *a priori* at 0.05. This procedure was also implemented in the computer program PC-ORD version 2.0 (MJM Software Design 1995).

To compare the total diatom abundance before and after each logging period, one way non-parametric Wilcoxon tests were used for each lake (Kruskal-Wallis). Non-parametric tests are useful to test whether group means or medians are the same across groups without assuming normality or homogeneity of variances. Non-parametric tests use functions of the response variable ranks, called rank scores. Multiple comparisons were done by ranking the data and performing an ANOVA on ranks followed by a Tukey-Krammer test.

A principal component analysis (PCA) was carried out on physical properties of the lakes and their individual watersheds to test whether any lake was different from the others based on physical characteristics. This procedure was run by using the computer program CANOCO 4.0 (ter Braak and Šmilauer 1998).

Results

Evaluation of model fit

From statistical screening for evaluation of fit of the model, we acquired significant justification for using the calibration model for all variables of interest such as pH, TP, TN, and DOC. The first approach showed a very good fit between the fossil and the modern diatom assemblages in terms of relative abundance of diatom taxa within the assemblage. In terms of analogs, in all three study lakes, 90 % of core samples felt under the 75% interval of confidence and therefore provide very good analogues. A total of 100 % of the diatom species assemblage (in all three-study cores) was represented in the modern calibration set. Likewise, examination of the dominant diatom fossil species indicated that these latter taxa were well represented in the modern calibration set with high effective occurrence or N2 values (from 16 to 49), suggesting that species assemblages in the model were compatible with those in the sediment cores.

The distributions of the squared residual distances of modern and fossil diatoms were skewed to the left in all lakes and for each variable. Therefore variables were log-transformed. One sample in Lac sans nom (depth 8 cm, 1940) and all samples in Lake Arthur (except at 9 cm depth, 1937) were outside the 90 % and 95 % confidence intervals and were considered as poor analogs in term of reliable variable reconstruction (Figure 6.3 and 6.4). In the Lac Arthur samples, the high abundance of *Tabellaria fenestrata* (Figure 6.4), attaining 40 %, was outside the mean of 2.5 % (standard deviation = 7.38) in the range of abundance for this taxa in the 76-lake modern calibration set (chapter I-Philibert and Prairie 2002a), contributing to the poor fit status.

A core sample was deemed a non analog when it was a poor analog for both the diatom assemblages in the modern calibration set and for the reconstructed variable (Laing et al. 1999). Thus, we suggest that part of the core section in Lac Arthur except at depth 9 cm (around 1937) must be interpreted with caution for all variables. Within core

samples providing less quantitative power for reconstructed values, utilization of ecology in the diatom stratigraphy provided a strong alternative for tracking the onset, magnitude and duration of any change occurring in the water bodies.

While the lack of close analogs in some core samples, as in Lac Arthur, indicated that our calibration model may not be a perfect match for all whole cores, the fits were close enough to justify the use of the previously developed transfer functions in chapter I (Philibert and Prairie 2002a).

Diatom composition changes and similarity results

A striking feature of the diatom flora was the dominance of the planktonic taxa in term of relative abundance. Planktonic taxa represented more than 50 % of the relative abundance in all sediment cores throughout the period of study. *Aulacoseira italica* var. *subarctica*, A. *lirata*, *Tabellaria fenestrata* and to a lesser extent *Cyclotella stelligera* dominated the assemblages in Lac sans nom and in L. Arthur (Figure 6.3 and 6.4) which had very similar species compositions. From their optima, the latter species reflected oligotrophic and neutral water conditions with low DOC values (< 10 $mg.l^{-1}$). Lac Rouillard was also dominated by planktonic taxa, the major taxa included *Asterionella formosa*, *Aulacoseira distans*, *A. lirata*, *A. perglabra* and *Tabellaria fenestrata* (Figure 6.5). The latter species were characterized by low trophic level (TP values less than < 10 $\mu g.l^{-1}$), neutral pH and low DOC concentrations (< 10 $mg.l^{-1}$) (chapter I- Philibert and Prairie 2002a).

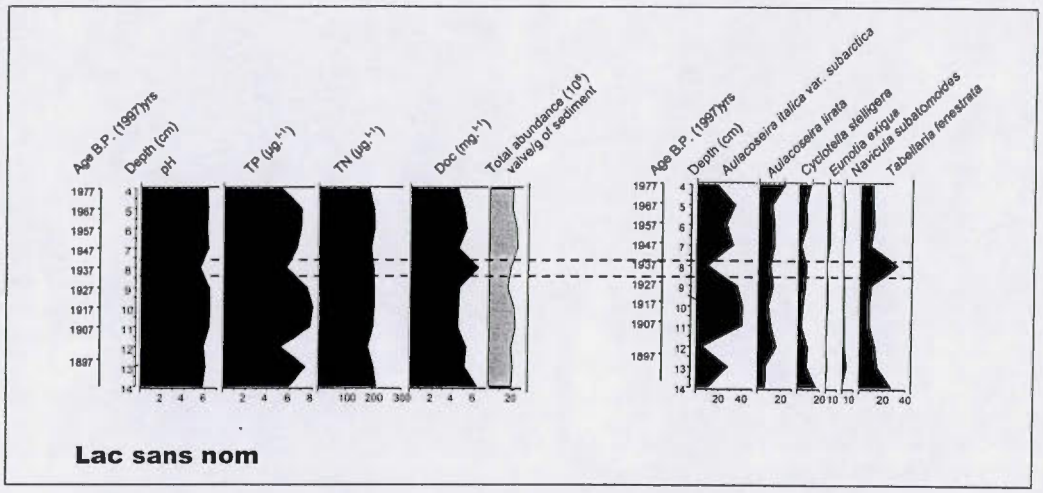

Figure 6.3 Stratigraphic diagram in Lac sans nom of diatom-inferred pH, TP, TN, and DOC values, the total abundance of diatoms (number of valves / g of sediment) and stratigraphical diagram of the relative abundance for main diatom species.

I.D.	lake	year of disturbance	LA	catchment	DA/LA	Z (m)	slope (%)	% catchment	geographical data
			km²	surface Km²				logged	
C1	Lac sans nom	1935-1940	0,29	4.48	13.9	6	18.9	60	48°12'30"N 74°36'30"W
C2	Lac Arthur	1950-1959	0,29	6.70	21.6	7	11.3	80	48°27'10"N 73°46'40"W
C3	Lac Rouillard	1940-1949	0,78	8.70	10.0	21	14.5	60	48°25'00"N 73°48'50"W

Table 6.1 Characteristics of catchments and disturbances that occurred in study lakes: DA drainage area LA: lake surface, Z: mean depth.

comparisons of levels:	preharvesting-harvesting	harvesting-postharvesting	preharvesting-postharvesting
logging C1 (from 1935-1940)			
T values	-2.180	-2.780	-0.118
probability (p)	0.0262*	0.017*	0.350
R	0.297	0.560	0.006
logging C2 (from 1950-1959)			
T values	0.330	-0.126	-0.042
probability (p)	0.617	0.494	0.343
R	-0.017	0.003	0.022
logging C3 (from 1940-1949)			
T values	-0.110	1.029	-4.150
probability (p)	0.387	0.860	0.001*
R	0.004	-0.070	0.085

Table 6.2: Test statisctic describing the separation between the groups.
The average within-group distance is compared with the inter-group distance. Euclidean distances are considered.
R= 1- ratio (within-group/inter-group) distance
Rmax = 1 when all items are identical withing groups
R < 0 when more heterogeneity within groups than inter-groups.

The null hypothesis of no difference between diatom assemblages before and after the onset of the logging period could not be rejected for Lac sans nom and L. Arthur based on the MRPP test ($p > 0.05$) (Table 6.2). Due to the high variability in relative abundance in *Aulacoseria lirata* and *Aulacoseira perglabra*, Lac Rouillard showed significantly different diatom assemblages before and after harvesting (Figure 6.5). However, Lac sans nom showed a significant difference in species assemblages before (or after) the logging relative to the partial logging period (1935-1940), whereas there was no significant variation in species composition in lakes Arthur and Rouillard (Table 6.2). During the logging period in Lac sans nom, there was a strong 175 % increase in *Tabellaria fenestrata* concurrent with a 133 % decline in *Aulacoseira italica* var. *subarctica* and a 20 % decrease in *Aulacoseira lirata*. In Lac sans nom, the species that contributed the most to the significant discrimination between the logging period and conditions prevailing before and after logging in terms of species composition (MRRP analysis) were *Aulacoseira italica*

var. *subarctica*, *Tabellaria fenestrata* (Indicator Species Analysis, $p < 0.05$) and to a lesser extent *A. lirata* (Figure 6.3) (Indicator Species Analysis, $p > 0.05$).

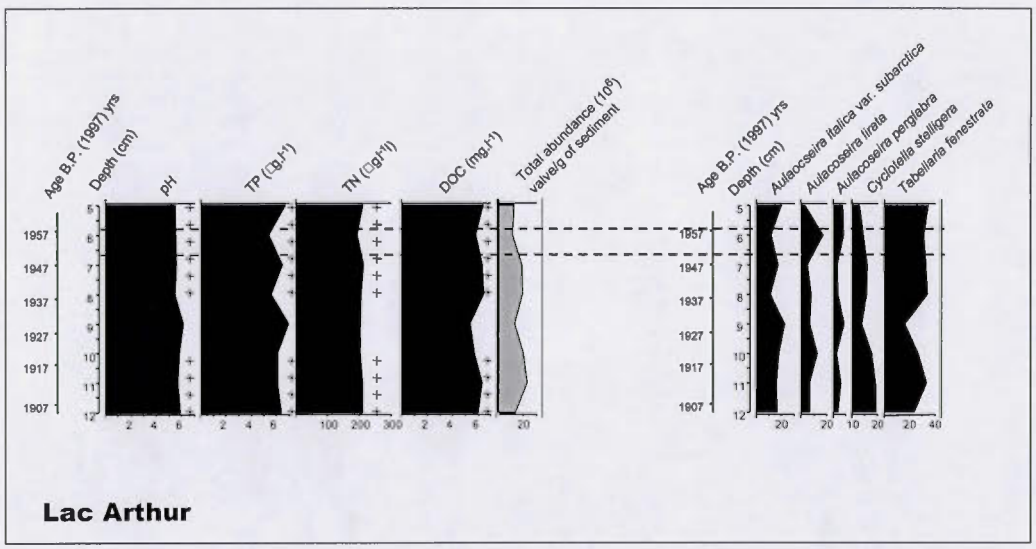

Figure 6.4 Stratigraphic diagram in Lake Arthur of diatom-inferred pH, TP, TN, DOC and CO_2 values, the total abundance of diatoms (number of valves /g of sediment) and stratigraphical diagram of the relative abundance for main diatom species.
Cross (+) indicated poor or no analogs.

In Lac Arthur the changes in diatom assemblages were subtle and exhibited a large variability along the sediment section we studied (Figure 6.4). The highest increase was reported for *Aulacoseira lirata* (100 %) concurrent with a very small decrease in *A. italica* var. *subarctica*. *Tabellaria fenestrata*, which made making up 40 % of the total relative abundance, did not vary during the partial logging period.

From fossil diatom remains, no change in species assemblages was reflected in the sediment core of Lac Rouillard. No variation was observed in dominant taxa such as *Asterionella formosa*, *Aulacoseira distans*, *A. lirata*, *A. perglabra* and *Tabellaria fenestrata* (Figure 6.5). The partial logging period was confounded by the natural variability over the end of the 19th and the 20th century.

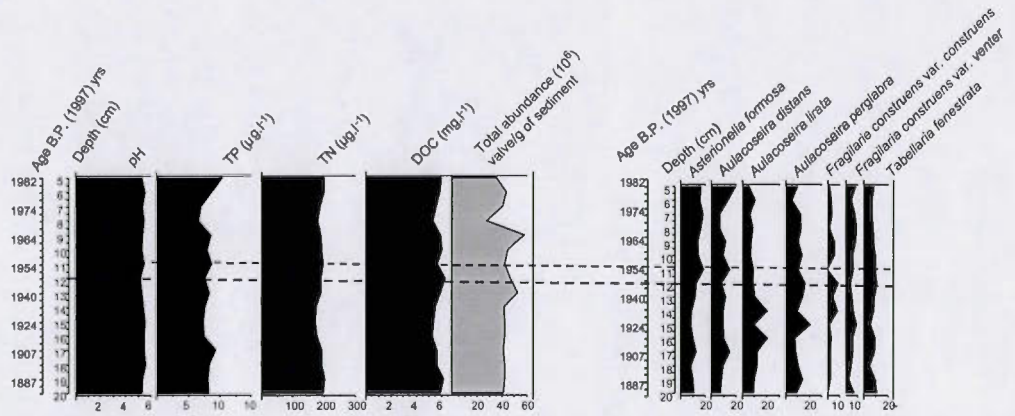

Figure 6.5 Stratigraphic diagram in Lake Rouillard of diatom-inferred pH, TP, TN, DOC and CO_2 values, the total abundance of diatoms (number of valves/g of sediment) and stratigraphic diagram of the relative abundance for main diatom species

The null hypothesis of no difference between total diatom abundance before and after the logging period was accepted in all three lakes (ANOVA test, $p > 0.05$) (Figures 6.3, 6.4, 6.5). There was not apparent shift in total diatom abundance

corresponded with the onset of logging either.

According to the exploratory PCA analysis (not shown here), the physical characteristics that significantly discriminates the Lac sans nom from the other lakes was the slope in the catchment but only the second Axis.

Reconstructed variables

All three lakes followed the same pattern in inferred-pH variation. The pH was constant at about 6 over the last 100 years. Similar patterns were observed for all lakes regarding TP (between 6 and 10 $\mu g.l^{-1}$), TN (200 $\mu g.l^{-1}$) and DOC (6-6.5 $mg.l^{-1}$). Over the last 100 years, the lakes have remained oligotrophic with low concentrations in TN. In Lac sans nom there was, however, a significant 37 % increase in DOC and a small although not significant decline in TP values during partial logging. No significant change was observed in Lac Arthur for each variable of interest between 1950 and 1959, neither in L. Rouillard from 1940 to 1949 corresponding with the periods of timber harvesting.

Discussion

Of the three lakes studied, only Lac sans nom showed a significant shift in diatom assemblage (*Aulacoseira italica* var. *subarctica* and *Tabellaria fenestrata* taxa) following forest harvesting. As a result, inferred DOC increased but even this change is somewhat speculative because *Aulacoseira italica* var. subarctica and *Tabellaria fenestrata* taxa favor low DOC conditions. Consequently, it is difficult to ascertain whether the increase in DOC was real or whether it could be attributed to either the cumulative change of some rare species or derived from poorly estimated optima in our modern calibration model in chapter I (Philibert and Prairie 2002a). For the other two lakes, no detectable changes were apparent neither in the diatoms nor in the inferred chemistry.

This general lack of response is surprising given that, for lakes of the same area, Carignan et al. (2000) showed that forest harvesting did produce some significant

increase in nutrient and DOC concentrations, increases that could have been detectable by the sensitive diatom flora. In their model, Carignan et al. (2000) could predict the magnitude of the nutrient response using a measure of the area extent of the perturbation relative to the lake volume or area. The application of this concept to our lakes suggest that Lac Arthur should have yielded the greatest effect (DA/LA = 13.9), which is clearly not the case here. Several factors could potentially explain the apparent lack of response, none of which can be completely eliminated.

First, it is possible that changes did occur but were either too small to be detected from diatom shifts. However, diatom-based reconstructions have been shown elsewhere to be adequate to identify and quantify nutrient increases of equivalent magnitude as those observed in lakes of the same region (Carignan et al. 2000; Prepas et al. 2001; Enache and Prairie 2000, Philibert, Prairie and Campbell, submitted). Moreover, we did not see any increase in total diatom abundance as predicted by Planas et al. (2000), something that should have been easy to identify.

Second, the effects may have been too short-lived. Indeed, our 1 cm sediment resolution corresponds to between 5 and 10 years of sedimentation in these lakes, which may be sufficient to swamp a short-lived effect. However, the lake where we have some evidence of an effect is Lac sans nom, where the swamping should have been greatest because of its low sedimentation rate (about 1mm/yr).

Third, it may be possible that the lakes suffered very little impact when partial logging was conducted in the drainage area. It is essential to realize that logging practices used in the middle of the past century differed markedly from modern methods and render a comparison with highly mechanized clearcutting at best unfair. We suggest that the main reason for the discrepancy between our results and those of Carignan et al. (2000) may not lie with the inadequacy of the paleolimnological approach but rather with the differential effect that old and modern timber harvesting technology may impart on surrounding lakes. The impact of forest activities on the catchment and implicitly on their aquatic portion probably depends on the type of harvesting. Depending on the

magnitude of harvesting, silvicultural practices can bring about a continuous succession in vegetation, a slowdown in re-vegetation or even a reversion to its initial status (Bergeron et al. 1999). For example, while up to 80% of the catchment may have been harvested, this was usually done over a span of a few years, rarely exceeding 20% per year (logging company, pers. comm.). In addition, this partial logging took place in the winter months, a common practice at that time, which is likely to have substantially mitigated soil erosion and reduced the associated nutrient transport from the drainage basin.

Finally, a recent study in nearby Abitibi (Québec) showed that partial cutting during the mid-20th century had little impact on forest structure and composition, and such practices could be integrated in long-term natural variability (Bescond 2002). Bergeron et al. (1999) built a table comparing natural disturbances with silvicultural practices. If clearcutting impacts match well with fire disturbances at different magnitudes, by reverting back the succession at its initial status, partial cuts may have effects similar to that of windthrows that create small gaps and mimic the natural mortality in undisturbed stands and is closer to natural succession (Bergeron et al. 1999). Short-term chemical responses of small streams to windthrow have been observed in the Experimental lakes Area (Schindler et al. 1980, Bayley et al. 1992) and showed a return to predisturbance levels within 3 years. Recent paleolimnological studies elsewhere in Canada (Paterson et al. 1998; Laird and Cumming 2001; Laird et al. 2001) had also concluded that the effects of forest logging other than clear-cutting were difficult to discern and /or small in magnitude. Our results also support this contention. However, if this is the consequence of less invasive harvesting practices and that the impacts of partial cutting are effectively undiscernable from natural variability, this may be an important lesson for sustainable forest management by supporting silvicultural practices based on partial cuts as an analog to natural perturbations which do not disturb the pre-established regeneration or soils (Bergeron et al. 1999). Analogously, Prepas et al. (2001) have shown that the effects of clearcutting could not be moderated by buffers strips around the lakes regardless of their width and therefore they were not effective in moderating changes in

water quality in disturbed drainage basins. We suggest that the comparative effects of partial harvesting versus clearcutting on lakes should be investigated further.

Acknowledgments

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Conclusion générale

Les contributions de cette thèse à de meilleures connaissances scientifiques peuvent être divisées en deux parties. Dans la première, les chapitres I et II examinent certaines questions fondamentales de la paléolimnologie en tant que discipline.

Ces contributions sont d'avantage théoriques même si elles soulèvent des applications d'ordre pratique. Dans la seconde partie, qui comprend les chapitres III, IV, V et VI, l'approche paléolimnologique à été utilisée dans le contexte des pratiques forestières en aménagement durable des forêts et de leurs impacts sur la qualité des eaux des lacs. Ces chapitres sont d'ordre pratique. Les points clés de cette thèse sont résumés selon les deux grandes approches fondamentales et pratiques.

Quelques nouvelles idées fondamentales en paléolimnologie

Une des premières contributions de cette thèse est le développement de deux nouvelles fonctions de transfert, ou modèles de prédictions, à partir de variables non communément utilisées en paléolimnologie, mais qui influencent inévitablement les assemblages de diatomées. Il s'agit de la concentration en CO_2 dans l'épilimnion (chapitre I). Alors que le développement de la variable CO_2 confirme tout d'abord la super saturation des lacs en CO_2, ceci met également l'accent sur l'origine des variations de concentrations entre les lacs. Le fait que cette super saturation est probablement due aux apports des eaux souterraines, la possibilité que cette variable environnementale puisse influencer les communautés diatomiques permettrait dans certains cas la reconstruction historique des changements en apports des eaux souterraines vers les lacs. Jusqu'à présent, ces apports restent difficiles à évaluer.

Cette thèse contribue également à l'établissement de deux nouveaux ensembles de calibration (chapitres I et III). Le premier se situe dans la province du Québec par l'extension d'un premier ensemble pré établi en Abitibi (Enache et Prairie 2002) avec des lacs de la région de la Haute Mauricie (Réservoir Gouin). Le second se trouve en Alberta. Les deux ensembles de calibration mettent en évidence de nouvelles flores de diatomées

modernes échantillonnées à la surface des sédiments de chaque lac, ainsi que deux nouveaux ensembles de données environnementales modernes à l'échelle des lacs comme du bassin versant (climat, géographie, géologie, topographie, physique, chimie et biologie).

A partir d'analyses statistiques, j'ai évalué les relations existantes entre l'abondance relative des diatomées modernes et des variables environnementales actuelles. Ainsi, une meilleure connaissance des caractéristiques écologiques des espèces de diatomées (optima, tolérance) est rendue possible dans les deux provinces.

Même si un grand nombre d'ensembles de calibrations développés dans la littérature ont permis une source d'information au sujet de la biogéographie, biodiversité et les relations espèces-variables, beaucoup de cette information cependant demeure non explorée. En conséquence, cette thèse a exploré certains principes de base en vue de valider et d'améliorer la performance des fonctions de transfert et ainsi permettre des reconstructions d'une plus grande fiabilité et de meilleure qualité (chapitre II). Ces fondements peuvent s'appliquer non seulement à la paléolimnologie mais également à d'autres domaines en écologie. En effet, même si le but premier en paléolimnologie est de prédire les conditions environnementales dans les eaux libres, la grande majorité des fonctions de transfert prennent en considération l'ensemble des taxa de diatomées (planctoniques, littoraux ou benthiques). Ce problème est particulièrement accru si l'on considère que dans la plupart des études, la majeure partie des espèces est de milieu benthique et non des eaux libres. En conséquence, cette thèse met l'accent sur cette controverse en testant si effectivement le fait d'intégrer toutes les espèces dans les modèles reste approprié et nécessaire pour la performance de ces modèles. Contrairement à nos attentes, les modèles basés uniquement sur les taxa planctoniques, ou encore les taxa directement en relation avec les variables environnementales mesurées, sont moins performants que ceux basés sur les taxa benthiques. En revanche, pour le même nombre d'espèces, les espèces planctoniques sont meilleurs prédicteurs et offrent d'avantage d'information que les taxa benthiques. Ces résultats démontrent que les taxa benthiques répondent directement ou indirectement aux changements de la

chimie des eaux libres. Ce chapitre II teste également d'autres principes fondamentaux en paléolimnologie, entre autre, celui qui soutient que les espèces qui possèdent une niche écologique restreinte (espèces rares ou de faible tolérance) auraient un pouvoir de prédiction très important. En premier lieu, on pourrait se poser la question suivante : est-ce que la tolérance estimée pour une variable est faible parce que les espèces sont recluses dans un milieu particulier avec des conditions environnementales spécifiques ou tout simplement la tolérance est mal estimée? Alors que la performance semble être reliée à l'ubiquité des taxa, les résultats de cette thèse amènent des doutes quant aux soi-disant attributs de la performance des modèles qui sont la tolérance des taxa et le nombre effectif d'occurrence ou N2. Outre ceci, il est clairement démontré dans ce chapitre que le nombre des espèces incorporé dans les modèles est un atout clé quant à leur performance.

Effets des perturbations du bassin versant sur la qualité des eaux des lacs : approche paléolimnologique.

Avec pour objectif premier de concilier à la fois une production effective du bois en termes de coûts ainsi que d'une productivité à long terme et du maintien de la biodiversité en forêt boréale, un nouveau concept en aménagement a été d'intégrer les perturbations d'origine naturelles comme anthropiques dans une politique de foresterie durable. Un consensus grandissant se veut de prendre comme modèle les perturbations naturelles pour les nouvelles pratiques forestières, en prenant pour acquis que des coupes qui imitent la fréquence et l'intensité des perturbations naturelles auraient un minimal d'impact sur l'écosystème. Un meilleur aménagement des ressources prendrait en considération tous les systèmes récepteurs de telles perturbations et notamment les bassins lacustres. L'attention particulière de cette thèse vise à reconstruire les impacts à long terme des feux de forêt et des coupes de forêt sur la biogéochimie des lacs en milieu boréal, mais aussi essayer de mettre au point des outils capables d'estimer les impacts des pratiques forestières versus les perturbations naturelles comme les feux.

Cette thèse met en comparaison deux provinces en milieu boréal canadien (le

Québec et l'Alberta). Si les deux provinces sont éloignées géographiquement, elles présentent aussi des caractéristiques limnologiques contrastées et ceci à plusieurs niveaux (géologie de surface, morphométrie, niveau trophique, etc....). Une telle comparaison est intéressante. Si les prédictions climatiques s'avèrent correctes, le cycle des feux de forêt va tendre à décroître dans l'est canadien mais aura tendance à s'accélérer en Ontario et dans les plaines boréales ou prairies de l'ouest canadien. Étant donné que le feu est l'agent de perturbation majeur en écosystème boréal, les changements d'intervalles de feux au Québec ou en Alberta vont modifier inévitablement le flux du matériel drainé du bassin versant en direction des lacs récepteurs.

Le chapitre III confirme le fait que les diatomées sont des indicateurs performants et utiles des feux de forêt en terme de changement des abondances relatives des espèces pour la détection, la durée et l'amplitude de telles perturbations. Même si je ne suis pas en mesure de reconstruire avec certitude les variables environnementales en raison de la faiblesse de nos fonctions de transfert en Alberta, il s'avère que les impacts des feux affectent significativement les assemblages de diatomées à Christina Lake avec un temps de retour à la normale inférieur ou égal à la période couvrant un centimètre de sédiment. Le rapport taxa benthiques versus taxa planctoniques ainsi que l'abondance totale des diatomées augmentent lors des événements de feux. Les feux n'affectent apparemment pas la richesse des espèces. J'en conclus que les taxa benthiques doivent prendre avantage de la faible tolérance des taxa planctoniques en condition lumineuse réduite provenant de l'apport des particules de charbon. Ce chapitre enfin soulève le problème de l'inter-compétition entre les espèces qui est encore mal connu et qui probablement affecte la variation des abondances relatives de certaines espèces présentant systématiquement des tendances inverses.

Le chapitre IV supporte également le fait que les diatomées sont de très bons agents de prédiction des événements de feux. Des augmentations rapides mais d'amplitude variées interviennent dans les concentrations reconstruites de CO_2 lors des perturbations de feux, identifiées par la stratigraphie des charbons au Lac Francis (Québec). Le temps de retour à la normale reste inférieur ou égal à la période couvrant un centimètre de

sédiment. Par conséquent, cette variable peut être considérée comme un outil en paléolimnologie pour la détection et l'intensité des feux et, implicitement, dans la fréquence des feux déterminée par les changements climatiques. Les augmentations à court terme dans les concentrations de phosphore total, ou PT, prouvent également leur aptitude comme outil en détection et intensité des feux. Le temps de retour à la normale reste encore inférieur ou égal à la période couvrant un centimètre de sédiment.

Dans le chapitre V, contrairement à l'étude similaire réalisée dans une forêt mixte au Lac Francis (chapitre IV), aucun changement n'a été observé dans la chimie du Lac à la Pessière pendant les événements de feux à l'exception d'une légère augmentation en CO_2 après un feu. Les résultats de ce chapitre révèlent que les changements de la chimie de l'eau induits par les feux sont faibles dans les bassins de drainage dominés par des forêts de conifères. Il est suggéré que l'excès d'humidité et la forte épaisseur d'humus limitent la mobilisation des nutriments et des ions majeurs pendant un feu. De plus, il est aussi important de noter que la différence d'intervalle de temps entre les feux peut agir en terme d'impact. Celui-ci est plus court au lac Francis qu'au Lac à la Pessière. En favorisant l'accumulation de la matière organique dans le bassin versant, l'intervalle de feu plus long au Lac à la Pessière peut ainsi réduire la couche de matière organique retirée lors d'un feu et, par conséquent entraîner une moins bonne exposition du sol minéral, limitant alors le drainage de matériaux en direction du lac. L'absence d'impact au Lac à la Pessière peut être aussi attribuée à la stabilité de la végétation dominante dans le bassin de drainage même après feu, et aussi, en raison du faible rapport aire du bassin de drainage sur celle du bassin lacustre, si l'on compare ces résultats à ceux du Lac Francis (chapitre IV).

Résumé des résultats : chapitres III, IV et V

Changements détectables après feux			
	Christina Lake	**Lac Francis**	**Lac à la Pessière**
	Forêt mixte		Forêt de Pessière
Changement de l'abondance relative des espèces majeures (Rhodes et Davis 1995, Korhola et al. 1996, Enache et Prairie 2000)	oui	oui	Non, excepté un pic de feu
Augmentation de l'abondance totale (Enache et Prairie 2000, Planas et al. 2000)	oui	oui	/
Augmentation du rapport BEN/PLA	oui	non	non
Augmentation de phosphore total (Bayley et al. 1992, Carignan et al. 2000, McEachern et al. 2000)	/	oui	non
Augmentation de CO_2 dissous	/	oui	Non, excepté un pic de feu
Augmentation d'azote total (Bayley et al. 1992, Carignan et al. 2000, McEachern et al. 2000)	/	non	non
Augmentation d'anions ou de cations (Carignan et al. 2000, McEachern et al. 2000)	/	non	non

Le chapitre VI démontre que si les coupes partielles du milieu du siècle dernier induisent bel et bien un changement dans la chimie des eaux des lacs, la détection, l'amplitude, ou encore la durée du changement n'est pas décelable à partir des communautés de diatomées (chapitre VI). De tels résultats sont expliqués par les anciennes techniques de coupes peu mécanisées et réalisées durant l'hiver diminuant ainsi toutes perturbations au sol comme au niveau de la régénération de la végétation pré établie. Ce chapitre met en perspective que si effectivement les impacts de coupes totales se rapprochent des feux de forêt en terme de perturbation en reportant les cohortes d'arbres en début de succession, les coupes partielles ont, quant à elles, des

effets similaires à ceux des chablis ou tombées d'arbres morts qui créent des trouées et, de cette façon, imitent la mortalité naturelle et se rapprochent de la succession végétative naturelle.

Perspectives futures

Sans perdre en considération les prédictions de réchauffement global au Québec comme en Alberta en terme de fréquence des feux, je suggère que d'autre études soient réalisées afin d'explorer les relations à long terme entre les processus aquatiques et terrestres en forêt boréale dépendamment des intervalles de feux en forêt mixte comme en forêt de conifères. Ainsi, il serait possible de déterminer à travers quels mécanismes le type de forêt agit au niveau de l'effet des feux sur les lacs récepteurs.

Finalement, si les anciennes pratiques forestières sont effectivement peu ou pas discernables de la variation naturelle en terme d'impact, c'est un atout dans une perspective d'aménagement forestier durable en prenant les coupes partielles comme analogues à des perturbations naturelles de faible impact tant bien sur le milieu terrestre que lacustre. Cependant, d'autres études seraient utiles afin d'évaluer l'impact des coupes partielles sur les lacs, mais cette fois-ci avec des pratiques forestières modernes et mécanisées.

La nature multidisciplinaire de la paléolimnologie et l'échelle à laquelle elle s'adresse au niveau de la pertinence d'application dans notre société, demeurent parmi les aspects les plus prometteurs de cette nouvelle science. Humblement, cette thèse apporte quelques nouveaux atouts dans cette discipline en pleine effervescence. Les nouvelles idées, méthodes, variables ou encore les implications pratiques contribuent, je l'espère, à l'expansion de cette discipline même s'il reste à confirmer ou tester certains fondements.

Ce travail tout au long de cette thèse nous a montré encore une fois, que la nature est plus complexe que l'on pouvait l'anticiper au début du projet.

Global conclusion

The contributions of this thesis to new scientific knowledge can be divided into two groups. In the first group, chapters I and II examine some fundamental issues of paleolimnology as a discipline. Their contributions are therefore more theoretical in nature although they have major practical implications. In the second group, which comprises chapters III, IV, V and VI, I used the paleolimnological approach in the context of sustainable forestry management practices and their effects on lake water quality. These chapters are therefore more applied by design. The main findings of the thesis are summarized below according to this chapter division.

Some new fundamental ideas for paleolimnology

One of the first contributions of this thesis is the development of two new diatom-based transfer functions from variables not commonly used in paleolimnology, but which inevitably influence diatom assemblages, such as the concentration of CO_2 in the lake water epilimnion (Chapter I). While the development of a CO_2 variable confirms firstly the supersaturation of lakes with CO_2, it secondly highlights lake-to-lake variations in CO_2 concentration origins. The fact that this supersaturation is likely due to groundwater inputs and the possibility that this environmental variable may be influencing diatom communities might allow, in some cases, the reconstruction of historical changes in groundwater inputs to lakes. This is an important characteristic of lakes that has proved difficult to reconstruct.

This thesis contributes to two new lake calibration sets (Chapters I and III) first for the Province of Québec, by extending the one in Abitibi (Enache and Prairie 2002) with lakes in Haute Mauricie (Réservoir Gouin), and second for Alberta. Both calibration sets offer two new modern diatom floras collected near the surface of lake sediments and two large new data sets of actual environmental variables (climate, geography, geology, topography, physics, chemistry, biology) at both lake and watershed scales. By evaluating the relationships between the relative abundance of modern diatoms and actual

environmental variables from statistical analyses, a better knowledge of diatom ecological characteristics (optima, tolerance) is thus reached for both provinces.

Despite the development of published modern calibration data sets, which provide a large amount of information about biogeography, biodiversity and species-variable relationships, much of this information remains unexplored. This thesis therefore endeavors to explore some of the underlying variables in order to validate and to perform predictive models for better and reliable reconstructions, not just in regard to paleolimnology but to other ecological issues as well (Chapter II). Indeed, the great majority of diatom-based transfer functions are based on complete diatom assemblages (pelagic, littoral and benthic), even if the stated purpose is to predict open-water chemical conditions. This problem may become particularly acute with paleolimnological calibrations based on diatoms since in most studies benthic diatoms often dominate the assemblages. The thesis highlights this controversy by questioning whether all taxa are appropriate and necessary to construct useful inference models. Contrary to our expectations, planktonic taxa, i.e. those diatoms that are in direct contact with the measured environmental characteristics of interest, are less apt to yield powerful predictive models than benthic ones. Therefore, while each individual planktonic species brings more useful predictive information than individual benthic species, the latter group nevertheless produces better models. The present thesis may change our perspective on the so-called poor predictor potential of benthic taxa expected in the literature (but not previously tested) and proves that benthic diatoms do respond, either directly or indirectly, to changes in open-water chemistry. This thesis in Chapter II also questions some fundamental principles in ecology behind the paleolimnological approach, i.e., that species with a narrow environmental niche (rare taxa or low tolerance) are particularly important. One first can question whether the estimated tolerance is small because the species is truly confined to specific environmental conditions or because the tolerance is poorly estimated. While the ability to hinder performance seems related to the ubiquity of taxa, the thesis clearly casts some doubt on the long-held view that species tolerance and the effective number of occurrences (N2)

is a key attribute in inference models. It is clearly demonstrated in this thesis that the number of species is the major factor in terms of performance.

Effects of landscape perturbations on lake water quality: a paleolimnological approach

With the main objective of conciliating both cost-effective wood production with long-term productivity and biodiversity maintenance in the boreal ecosystem, a new concept in management has been to integrate both natural and human disturbances into the framework for sustainable forestry. A growing consensus is that harvest practices modelled on the characteristics of natural disturbances are most likely sustainable when they mimic the frequency and the extent of such disturbances. For a better management of resources a relevant sustainable management must take into account all the impacts of such disturbances on the receptor ecosystems i.e. lakes. The avenue being given attention in this thesis is to reconstruct the long-term impacts of logging and of wildfires on the biogeochemistry of lakes and the establishment of tools capable of estimating the impacts of logging practices relative to those of comparable natural disturbances.

The thesis compares the effects of fire for two different provinces (Quebec and Alberta) far removed geographically and with greatly contrasting limnological characteristics (surface geology, morphometry, nutrient condition, etc...). Such comparison is interesting because if climatic forecasts are correct, the forest fire cycle is likely to decrease in the Canadian Eastern part but increase in Ontario as well as in the Boreal Plain in the Prairies. Because fire is arguably the main disturbance in boreal terrestrial ecosystems, the expected lengthening of the fire cycle in Quebec or in Alberta will likely modify the storage and the flux of nutrients, organic carbon and water between lakes and their catchments.

Chapter III supports that diatoms are a good and useful indicator of fire disturbances in terms of species change for the detection, duration and magnitude of the event in Christina Lake (Alberta). Even if I was not able to compare the magnitude of change in

environmental variables due to the weakness of our predictive models in Alberta, the impacts of fire are significantly detected from changes in diatom assemblages with a time recovery inferior to the time frame of one-centimetre of sediment core. The benthic: planktonic taxa ratio increases as does the total diatom abundance following a fire, but no detectable impact on the species richness is observed. It is concluded that benthic taxa must take advantage of fire disturbances by inputs of charcoal into the planktonic area where taxa are low lightly tolerant. This chapter questions also the issue of the inter-species competition which appears to be a prime candidate in diatom assemblage variation. Indeed, the fire-induced change in diatom assemblages seems to be superimposed on underlying interspecies competitions, which leads to a relative abundance for some species for reasons unconnected to the deforestation surrounding the lake.

Chapter IV supports that diatoms are a good and useful indicator of fire events. Short-term diatom inferred CO_2 pulses of varying magnitude are found and clearly associated with forest fires, as identified by charcoal stratigraphy in Lac Francis (Quebec). Due to the fact that CO_2 recovery is generally equal or inferior to the time frame covered by 1 cm of sediment, this variable may be a useful tool for detecting fire through paleolimnology and implicitly the frequency of fire events brought about by climatic changes. Short term TP pulses derived from diatom-based reconstruction have also proved their aptitude as a tool in detecting fire events, and still with a recovery generally equal or inferior to the time frame covered by 1 cm of sediment.

In chapter V, contrary to the similar study carried out in a mixed-wood forest surrounding Lac Francis (chapter IV), no changes were observed in the chemistry of Lac à la Pessière during fire events except, possibly, for CO_2 in one fire event. The results suggest that fire-induced changes in lake chemistry are small in catchments dominated by conifers. I suggest that this may be the result of excess moisture and the thick humus layer, which likely limits the mobilization of nutrients and major ions during a fire event. The lack of response in Lac à la Pessière may also be attributable to the stability of the vegetational composition in the catchment after fires and its lower

drainage ratio when compared with L. Francis (chapter IV). Finally a possibly confounding factor is the average time interval between fires that is shorter around L. Francis than it is at L. à la Pessière. By promoting the accumulation of organic matter in the catchment, the longer interval in L. à la Pessière may reduce the amount of matter removed by fire and thus less mineral soil becomes exposed, thereby preventing the drainage of materials into the lake.

Summary of results in chapters III, IV and V

Significant changes after fire			
	Christina Lake	**Lac Francis**	**Lac à la Pessière**
	Mixedwood forest	Mixedwood forest	Picea-moss forest
Changes in relative abundance of major species (Rhodes et Davis 1995, Korhola et al. 1996, Enache et Prairie 2000)	yes	yes	No, excepted For one event
Increase in total abundance (Enache et Prairie 2000, Planas et al. 2000)	yes	yes	/
Increase of the ratio BEN/PLA	yes	no	no
Increase in total phosphorus (Bayley et al. 1992, Carignan et al. 2000, McEachern et al. 2000)	/	yes	no
Increase in total nitrogen (Bayley et al. 1992, Carignan et al. 2000, McEachern et al. 2000)	/	yes	No excepted for one event
Increase in dissolved CO_2	/	no	no
Increase in anions and cations (Carignan et al. 2000, McEachern et al. 2000)	/	no	no

Chapter VI shows that if the partial loggings of the mid 20th century induced a change in lake chemistry, the magnitude or the duration of the change is too small to be

detectable from diatom assemblages (Chapter VI). I explain such results by the old partial logging techniques that prevented any disturbances in the soil and pre-established vegetative regeneration, especially when conducted during the winter. This chapter puts into perspective that if the impacts of clear cutting are similar to fire disturbances at different magnitudes, then by reverting the forest growth back to its initial status, partial logging has effects similar to that of wind-throws in that it creates small gaps and mimics natural mortality in undisturbed stands and is thus closer to the natural developmental processes.

General Perspectives

Regardless of the accuracy of the global warming predictions in Alberta and Quebec, I suggest that more studies are needed to explore the long-term relationships between the terrestrial and aquatic processes within the boreal forest in regards to fire intervals in mixed-wood forests as well as in closed crown coniferous forests, to evaluate through which mechanism forest composition modulates the effects of forest fires on the lakes into which they drain.

Finally if less invasive harvesting practices are effectively indiscernible from natural variability, this may be an important lesson for sustainable forest management by supporting silvicultural practices based on partial cuts as an analog to natural perturbations which do not disturb the pre-established regeneration of soils and implicitly lake water quality. However, more studies are needed to assess the impacts of modern and mechanized partial cuts on the biogeochemistry on lakes.

The intrinsically multi-disciplinary nature of paleolimnology and the scale at which it can pose questions of societal relevance are among the most promising aspects of this new science. This thesis humbly adds to this still emerging field. The new ideas, methods, variables and practical implications that it proposes have contributed to widening the field further, although they will undoubtedly require further testing and

refinements. The work developed in this thesis has shown us that, once again, nature is more complex than what can be anticipated at the onset of a project.

Appendix 1

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH	TP $\mu g.l^{-1}$	TN $\mu g.l^{-1}$	DOC $mg.l^{-1}$	CO_2 µM
Achnanthes 1 not identified	1	.	1	6.48	12.31	311.75	7.11	34.89
Achnanthes biasolettiana (Grunow) Cleve and Grunow	2	1	.	7.28	17.25	269.25	9.05	59.57
Achnanthes bioretii Germain	3	2	.	6.08	9.32	305.11	10.65	420.82
Achnanthes carissima (Lange-Bertalot) Lange-Bertalot and Krammer	4	.	1	6.71	14.46	275.23	10.58	40.03
Achnanthes catenata Bily and Marvan	5	2	.	6.00	10.10	362.78	12.43	21.37
Achnanthes flexella var. *alpestris* Brun	6	3	.	6.35	12.75	426.68	11.05	158.95
Achnanthes flexella var. *flexella* (Cleve) Cleve-Euler	7	1	.	7.80	6.25	128.50	4.45	21.37
Achnanthes joursacense Heribaud	8	1	.	6.75	6.75	135.75	8.55	49.29
Achnanthes kriegeri krasske	9	.	1	6.51	5.01	138.26	2.70	29.95
Achnanthes lanceolata var. *rostrata* (Oestrup) Lange-Bertalot	10	1	2	6.71	14.42	263.33	9.47	41.36
Achnanthes minutissima var. *affinis* (Lange-Bertalot) L.B. and K.	11	.	1	6.33	7.01	194.16	5.18	37.34
Achnanthes minutissima var. minutissima Kützing	12	24	17	6.72	12.67	365.78	9.81	107.47
Achnanthes oblongell a Oestrup	13	2	.	5.95	14.99	306.59	13.65	151.95
Achnanthes pusilla (Grunow) De Toni	14	3	.	7.04	14.08	274.92	8.56	91.51
Achnanthes ventralis (Krasske) Lange-Bertalot	15	4	.	7.45	8.29	217.75	6.70	58.69
Achnanthes ziegleri Lange-Bertalot	16	2	.	7.73	9.68	134.49	4.35	148.91
Actinella punctata Lewis	17	5	.	5.20	11.79	203.08	7.10	312.99
Amphicampa hemicyclus (Ehrenberg) Karsten	18	6	.	5.58	8.08	301.83	9.43	346.24
Amphipleura pellucida (Kützing) Kützing	19	1	.	7.28	17.25	269.25	9.05	59.57
Amphora ovalis (Kützing) Kützing	20	7	.	6.80	15.37	293.97	10.54	167.26
Amphora pediculus var. *pediculus* (Kützing) Cleve	21	1	.	8.01	7.00	79.00	2.94	28.78
Amphora thumensis (Mayer) Cleve	22	1	.	8.01	7.00	79.00	2.94	28.78
Anomoeoneis aponina Kützing	23	.	2	5.91	10.41	291.11	10.18	73.18
Anomoeoneis brachysira Brébisson	24	.	1	6.48	12.31	311.75	7.11	34.89
Anomoeoneis follis (Ehrenberg) Cleve	25	1	.	5.94	12.00	424.50	9.72	203.92
Anomoeoneis serians (Brébisson) Cleve	26	1	.	5.21	11.50	376.00	10.07	250.29
Anomoeoneis vitrea (Grunow) Ross	27	.	1	6.72	11.99	316.69	8.02	33.82
Asterionella formosa Hassall	28	12	29	6.08	8.53	254.31	6.09	94.85
Aulacoseira 1 not identified	29	3	.	5.70	8.90	269.14	8.38	300.66
Aulacoseira 2 not identified	30	4	.	6.00	8.43	236.01	7.24	94.41
Aulacoseira alpigena (Grunow) Krammer	31	.	17	6.47	8.91	258.02	6.70	39.56
Aulacoseira ambigua (Grunow) Simonsen	32	11	.	6.47	20.92	386.75	11.24	162.69
Aulacoseira distans var. *distans* (Ehrenberg) Simonsen	33	13	9	6.53	14.34	279.05	8.52	86.22
Aulacoseira distans var. *humilis* Cleve-Euler	34	14	.	6.34	13.36	331.27	12.65	165.28
Aulacoseira distans var. *nivalis* (W.Smith) Haworth	35	2	.	6.60	9.71	170.83	11.10	89.87
Aulacoseira distans var. *nivaloides* Camburn	36	11	.	5.98	11.77	326.51	11.59	290.96
Aulacoseira distans var. *tenella* (Nygaard) Florin	37	20	12	6.17	14.34	359.51	9.39	175.59
Aulacoseira italica var. *subarctica* (O.Müller) Simonsen	38	6	32	6.51	9.37	253.97	5.73	39.71
Aulacoseira italica var. *tenuissima* (Grunow) Simonsen	39	2	.	7.00	23.35	282.28	9.27	67.95
Aulacoseira lacustris (Grunow) Krammer	40	1	.	4.16	9.00	246.00	9.22	147.59
Aulacoseira lirata (Ehrenberg) Ross	41	10	15	6.20	6.55	202.22	5.06	78.14
Aulacoseira lirata var. *biseriata* (Grunow) Haworth	42	2	.	5.49	5.30	239.97	8.19	698.75
Aulacoseira nygaardii Camburn	43	5	.	5.33	6.99	233.01	8.24	335.96
Aulacoseira perglabra (Oestrup) Haworth	44	10	6	5.32	7.28	221.86	6.94	141.69
Aulacoseira perglabra var. *floriniae* Camburn	45	4	.	5.74	5.29	148.93	4.92	164.84
Aulacoseira tenuior (Grunow)	46	4	1	5.89	11.41	332.46	9.93	318.42
Brachysira brebissonii 1 not identified	47	19	13	6.07	9.21	294.80	7.94	150.44
Brachysira brebissonii 3 not identified	48	1	.	5.94	12.00	424.50	9.72	203.92
Brachysira procera Lange-Bertalot	49	2	.	6.30	10.71	324.34	8.25	165.79
Brachysira styriaca (Grunow) Hustedt	50	2	.	6.46	10.69	449.57	13.07	127.17
Brachysira vitrea (Grunow) Ross	51	14	.	6.78	14.71	647.01	11.12	85.10
Caloneis silicula (Ehrenberg) Cleve	52	.	1	6.54	10.46	252.02	4.33	28.04
Cocconeis placentula var. *euglypta* Ehrenberg	53	1	.	7.40	25.75	303.75	5.65	197.69

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH	TP µg.l^{-1}	TN µg.l^{-1}	DOC mg.l^{-1}	CO_2 µM
Cyclotella antiqua W. Smith	*54*	1	.	7.40	25.75	303.75	5.65	197.69
Cyclotella bodanic a Grunow	*55*	2	.	6.89	12.95	185.78	9.15	51.88
Cyclotella bodanica var. *lamanica* (O.Müller) Bachmann	*56*	11	25	6.63	7.83	246.66	7.00	45.57
Cyclotella comensis Grunow	*57*	.	8	6.39	10.70	259.71	8.12	50.11
Cyclotella distinguenda Hustedt	*58*	.	1	6.28	16.45	556.18	6.14	40.24
Cyclotella gamma Skvortow	*59*	1	.	7.80	6.25	128.50	4.45	21.37
Cyclotella glomerata Bachmann	*60*	.	3	6.43	7.86	249.34	5.25	31.92
Cyclotella meneghiniana Kützing	*61*	4	1	6.69	6.21	193.66	5.35	68.46
Cyclotella michiganiana Skvortzow	*62*	7	.	7.08	8.61	294.61	11.05	53.86
Cyclotella ocellata Pantocsek	*63*	5	6	6.73	6.82	212.64	5.35	37.38
Cyclotella pseudostelligera 1 not identified	*64*	7	1	6.32	9.77	380.12	12.34	101.15
Cyclotella psaudostelligera 3 not identified	*65*	5	.	7.06	13.33	610.40	11.79	47.47
Cyclotella rossii Håkansson	*66*	.	3	8.74	6.64	204.26	3.90	32.61
Cyclotella stelligera 1 not identified	*67*	13	25	6.49	8.43	263.86	7.14	64.46
Cyclotella stelligera 3 not identified	*68*	1	.	6.12	9.50	416.00	15.29	165.34
Cyclotella stailigeroides Hustedt	*69*	2	.	6.26	9.06	399.65	14.44	147.73
Cymbella aequalis W. Smith	*70*	1	.	6.95	12.00	501.50	14.10	68.00
Cymbella cesatii (Rabenhorst) Grunow	*71*	1	.	7.57	26.00	1489.50	14.74	12.73
Cymbella delicatula Kützing	*72*	2	.	7.58	24.97	1418.65	14.20	13.18
Cymbella gaeumannii Meister	*73*	10	.	5.62	9.76	249.81	8.66	336.45
Cymbella gracilis (Ehrenberg) Kützing	*74*	6	3	6.17	12.89	373.32	11.61	127.42
Cymbella hebridica (Grunow) Cleve	*75*	8	1	5.18	6.67	230.37	8.61	586.77
Cymbella incerta (Grunow) Cleve	*76*	5	.	6.39	10.29	342.91	8.68	141.05
Cymbella microcephala Grunow	*77*	7	1	6.53	15.29	537.68	10.27	248.09
Cymbella minuta Hilse	*78*	1	.	4.54	5.50	105.00	4.15	1037.45
Cymbella naviculiformis Auerswald	*79*	1	.	6.59	17.00	593.50	13.96	170.10
Cymbella silesiaca Bleisch	*80*	4	5	6.31	10.17	286.08	7.52	80.30
Denticula elegans Kützing	*81*	3	.	7.30	17.46	889.82	13.39	39.38
Diploneis elliptica (Kützing) Cleve	*82*	.	1	6.71	14.46	275.23	10.58	40.03
Diploneis modica Hustedt	*83*	3	.	6.59	13.80	306.97	9.79	262.80
Diploneis ovalis (Hilse) Cleve	*84*	3	.	7.16	18.62	309.53	9.85	50.95
Diploneis puella (Schumann)	*85*	2	.	6.74	10.85	325.40	12.76	77.96
Eunotia arculus (Grunow) Lange-Bertalot	*86*	.	1	5.90	12.17	337.91	12.68	88.03
Eunotia arcus Ehrenberg	*87*	1	.	6.95	12.00	501.50	14.10	68.00
Eunotia bidentula Schumann	*88*	7	.	4.66	7.09	195.45	7.17	533.94
Eunotia bilunaris (Ehrenberg) Mills	*89*	10	.	5.20	10.65	200.48	7.59	502.37
Eunotia bilunaris var. *mucophyla* Lange-Bertalot and Nörpel	*90*	6	12	6.01	10.70	293.98	6.61	139.73
Eunotia caroline Patrick	*91*	1	.	5.21	11.50	376.00	10.07	250.29
Eunotia elegans Oestrup	*92*	.	1	6.33	7.01	194.16	5.18	37.34
Eunotia exigua (Brébisson) Rabenhorst	*93*	5	2	5.93	13.62	349.60	8.99	198.68
Eunotia exigua var. *bidans* Hustedt	*94*	.	2	6.36	8.54	234.74	6.81	42.92
Eunotia faba Ehrenberg	*95*	2	4	5.85	10.44	267.18	6.50	291.56
Eunotia flaxuosa (Brébisson) (Kützing)	*96*	1	1	6.65	18.96	320.83	9.16	142.86
Eunotia glacialis Meister	*97*	.	2	6.63	11.12	295.59	8.33	36.62
Eunotia hemicylcus (Ehrenberg) Ralfs	*98*	.	1	6.34	6.11	226.05	4.76	32.68
Eunotia implicata Nörpel et al.	*99*	2	.	6.56	21.67	351.54	8.23	197.69
Eunotia incisa Gregory	*100*	7	13	6.14	9.69	268.51	7.96	103.35
Eunotia linearis Okuno	*101*	.	4	6.31	8.72	249.75	6.31	41.95
Eunotia meisteri Hustedt	*102*	1	1	6.68	10.57	318.67	10.41	64.11
Eunotia microcephala Krasske	*103*	2	.	5.66	11.53	240.74	10.42	287.78
Eunotia minor (Kützing) Grunow	*104*	1	2	5.38	6.70	189.24	4.68	521.36
Eunotia naegelii Migula	*105*	.	1	6.40	7.88	249.23	5.25	32.13
Eunotia nymanniana Grunow	*106*	2	.	5.15	9.11	304.69	10.01	344.09

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH	TP µg.l^{-1}	TN µg.l^{-1}	DOC mg.l^{-1}	CO_2 µM
Eunotia paludosa Grunow	*107*	5	2	6.43	13.65	264.29	8.16	180.40
Eunotia pectinalis (Dillwyn) Rabenhorst	*108*	.	9	6.38	10.74	296.30	6.29	38.93
Eunotia pectinalis var. *ventralis* (Ehrenberg) Hustedt	*109*	7	.	5.18	9.39	179.58	7.10	295.24
Eunotia pirla Carter	*110*	4	.	4.73	4.87	123.77	4.46	684.71
Eunotia polyglyphis Grunow	*111*	5	.	6.67	21.42	299.16	7.49	238.45
Eunotia praerupta Ehrenberg	*112*	2	.	7.05	14.22	657.83	14.20	59.25
Eunotia pyramidata Hustedt	*113*	.	2	5.98	8.05	251.87	5.06	42.54
Eunotia rhomboidea Hustedt	*114*	8	.	4.84	7.48	191.06	6.95	684.16
Eunotia rhynchocephala Krasske	*115*	4	.	5.64	9.24	360.35	11.40	254.68
Eunotia schwabei Krasske	*116*	.	3	6.37	10.00	273.57	6.41	36.03
Eunotia seminulum (Nörpel) Lange-Bertalot	*117*	.	1	6.61	5.33	176.47	5.23	28.57
Eunotia septentrionalis Oestrup	*118*	2	.	5.34	11.88	374.29	11.54	271.98
Eunotia serra Ehrenberg	*119*	3	1	5.60	9.58	178.73	4.46	231.58
Eunotia serra var. *diaderma* (Ehrenberg) Patrick	*120*	.	1	6.22	9.90	274.65	8.92	50.09
Eunotia subarcuatoides Alles et al.	*121*	1	5	5.99	8.91	269.56	9.13	180.70
Eunotia sudetica O.Müller	*122*	2	.	4.95	8.38	214.74	8.18	736.75
Eunotia tenera W. Smith	*123*	16	.	6.74	15.06	299.78	9.77	192.06
Fragilaria brevistriata 1 not identified	*124*	7	.	6.73	13.73	358.31	12.12	352.23
Fragilaria brevistriata 2 not identified	*125*	2	.	7.96	6.83	90.44	3.29	27.07
Fragilaria brevistriata 3 Grunow	*126*	4	5	6.67	11.79	276.08	7.39	59.29
Fragilaria capucina Desmazières	*127*	4	.	5.44	12.08	321.58	10.52	315.27
Fragilaria constricta Ehrenberg	*128*	4	.	4.99	10.97	238.48	8.90	546.09
Fragilaria constricta var. *stricta* Cleve	*129*	1	2	6.60	12.34	318.63	9.69	176.68
Fragilaria construens var. *binodis* (Ehrenberg) Grunow	*130*	13	4	6.89	10.75	263.28	8.26	190.95
Fragilaria construens var. *construens* (Ehrenberg) Grunow	*131*	0	1	7.04	7.48	168.22	4.71	44.46
Fragilaria construens var. *spiranum* (Ehrenberg) Grunow	*132*	1	1	6.74	5.70	224.03	6.21	39.08
Fragilaria construens var. *venter* (Ehrenberg) Grunow	*133*	3	11	6.27	12.42	305.01	5.57	73.82
Fragilaria crotonensis Kitton	*134*	.	1	6.40	5.25	172.85	3.58	37.48
Fragilaria exigua Grunow	*135*	.	1	6.74	5.70	224.03	6.21	39.08
Fragilaria fasciculata (Agardh) Lange-Bertalot	*136*	4	2	5.73	9.79	291.82	9.65	333.88
Fragilaria inflata Pantocsek	*137*	1	.	5.44	8.00	342.50	10.95	249.18
Fragilaria inflata var. *istranii* Pantocsek	*138*	1	.	7.30	30.50	327.25	10.85	59.18
Fragilaria intermedia Grunow	*139*	5	.	7.24	10.47	230.23	7.75	194.39
Fragilaria lapponica Grunow	*140*	1	.	5.39	16.00	418.00	11.81	.
Fragilaria lata (Cleve-Euler) Renberg	*141*	9	.	6.65	17.09	264.64	7.90	142.37
Fragilaria nanana Lange-Bertalot	*142*	5	.	6.41	11.64	245.29	9.72	340.30
Fragilaria pinnata Ehrenberg	*143*	.	2	6.69	7.01	219.04	5.48	30.42
Fragilaria pinnata var. *pinata* Ehrenberg	*144*	10	.	7.19	12.16	254.33	8.11	223.60
Fragilaria pseudoconstruens Marciniak	*145*	.	1	6.44	10.05	247.52	4.40	27.52
Fragilaria vaucheriae (Kützing) Petersen	*146*	.	1	6.51	5.01	138.26	2.70	29.95
Fragilaria virescens var. *exigua* Grunow	*147*	15	.	5.90	7.96	273.15	8.53	278.41
Fragilaria 1 not identified	*148*	.	1	6.28	16.45	556.18	6.14	40.24
Frustulia rhomboides 1 not identified	*149*	.	2	6.16	9.98	287.07	9.46	61.10
Frustulia rhomboides 3 not identified	*150*	.	24	6.28	9.03	266.12	8.74	48.00
Frustulia rhomboides var. *amphipleuroides* (Grunow) De Toni	*151*	1	.	4.60	5.00	181.00	8.00	853.27
Frustulia rhomboides var. *crassinervia* (Brébisson) Ross	*152*	24	.	5.47	10.49	263.63	8.07	322.47
Frustulia rhomboides var. *saxonica* (Rabenhorst) De Toni	*153*	2	.	4.59	11.46	306.54	10.13	147.59
Gomphonema 1 not identified	*154*	1	.	6.80	7.50	328.00	14.60	54.78
Gomphonema angustatum Agardh	*155*	.	2	6.37	7.12	212.49	4.88	32.51
Gomphonema gracile Ehrenberg	*156*	4	3	6.77	11.51	234.04	7.60	93.89
Gomphonema parvulum (Kützing) Kützing	*157*	2	.	6.67	14.41	227.26	5.86	138.97
Gomphonema subtile Ehrenberg	*158*	2	.	6.93	12.33	467.95	14.02	71.94
Navicula 1 not identified	*159*	4	.	7.46	13.81	655.44	10.66	31.46

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH	TP µg.l^{-1}	TN µg.l^{-1}	DOC mg.l^{-1}	CO_2 µM
Navicula 2 not identified	*160*	3	.	6.73	11.17	225.12	7.30	82.92
Navicula brachysira Brébisson	*161*	4	.	5.86	11.29	380.36	12.00	245.71
Navicula bulnheimii Grunow	*162*	.	1	6.95	7.00	216.10	4.40	35.20
Navicula cocconeiformis Gregory	*163*	3	.	6.57	10.45	401.82	14.94	147.95
Navicula cryptocephala Kützing	*164*	2	.	7.31	19.61	278.83	8.11	97.94
Navicula cryptotenella Lange-Bertalot	*165*	4	.	7.31	19.26	630.97	9.93	67.20
Navicula diluviana Krasske	*166*	2	.	7.95	6.79	93.16	3.37	26.66
Navicula indifferans Hustedt	*167*	.	1	6.40	5.25	172.85	3.58	37.48
Navicula kuelbsii Lange-Bertalot	*168*	.	1	6.71	14.46	275.23	10.58	40.03
Navicula laevissima Kützing	*169*	9	.	6.45	12.16	389.43	11.89	106.70
Navicula leptostriata Jørgensen	*170*	4	.	6.10	13.08	450.64	14.21	74.24
Navicula mediocris Krasske	*171*	5	.	6.12	10.18	337.74	9.27	149.42
Navicula molestiformis Hustedt	*172*	.	3	6.24	9.84	279.80	9.23	56.03
Navicula pupula Kützing	*173*	9	1	6.73	11.88	332.81	9.31	85.94
Navicula radiosa Kützing	*174*	7	4	6.71	12.98	290.86	8.62	65.88
Navicula scutiformis Grunow	*175*	.	1	6.43	6.02	239.16	6.75	38.01
Navicula seminuloides Grunow	*176*	3	.	6.37	11.58	253.84	8.31	115.20
Navicula seminulum Grunow	*177*	1	.	6.09	16.50	501.00	16.73	703.78
Navicula soehrensis var. *muscicola* (Petersen) Krasske	*178*	.	1	6.43	6.02	239.16	6.75	38.01
Navicula stroemii Hustedt	*179*	1	.	7.30	30.50	327.25	10.85	59.18
Navicula subatomoides Hustedt	*180*	6	3	6.50	12.14	272.34	7.86	181.55
Navicula subtilissima Cleve	*181*	9	2	5.40	10.90	354.55	9.74	247.95
Navicula viridula (Kützing) A94	*182*	1	.	7.80	6.25	128.50	4.45	21.37
Neidium ampliatum (Ehrenberg) Krammer	*183*	10	1	5.09	8.26	224.87	6.94	483.53
Neidium iridis (Ehrenberg) Cleve	*184*	9	.	5.04	6.66	171.20	4.87	353.38
Nitzschia minutula Grunow	*185*	11	.	6.46	12.55	358.10	10.43	225.58
Nitzschia fonticola Grunow	*186*	7	1	6.35	12.73	543.83	11.05	79.67
Pinnularia 1 not identified	*187*	3	.	4.91	8.21	269.21	8.08	448.34
Pinnularia biceps Gregory	*188*	.	1	6.40	7.88	249.23	5.25	32.13
Pinnularia braunii (Grunow) Cleve	*189*	14	.	5.30	7.99	219.66	7.22	618.53
Pinnularia divergens W. Smith	*190*	.	2	6.52	10.39	251.21	4.34	27.95
Pinnularia gibba Ehrenberg	*191*	12	1	5.81	12.19	283.38	8.55	292.07
Pinnularia interrupta W. Smith	*192*	3	.	6.00	11.76	357.94	11.84	192.89
Pinnularia maior (Kützing) Rabenhorst	*193*	5	3	6.50	13.13	350.79	9.70	187.40
Pinnularia mesolepta (Ehrenberg) W. Smith	*194*	.	1	6.54	10.46	252.02	4.33	28.04
Pinnularia microstauron 1 Ehrenberg	*195*	5	1	5.84	9.34	237.40	6.81	167.58
Pinnularia microstauron 2 Ehrenberg	*196*	11	.	5.63	10.30	293.03	9.17	438.10
Pinnularia schoenfelderii Krammer	*197*	.	3	6.54	10.56	247.83	5.28	30.34
Pinnularia viridis (Nitzsch) Ehrenberg	*198*	4	.	5.24	7.90	208.78	6.09	389.54
Stauroneis agrestis Petersen	*199*	6	.	5.70	12.07	357.60	12.40	423.41
Stauroneis ancaps Ehrenberg	*200*	.	2	6.58	10.27	288.53	6.87	33.12
Stauroneis gracilis Ehrenberg	*201*	.	1	6.54	10.46	252.02	4.33	28.04
Stauroneis phoenicenteron (Nitzsch) Ehrenberg	*202*	9	1	6.04	10.14	312.75	8.84	291.27
Stauroneis producta Grunow	*203*	.	1	5.90	12.17	337.91	12.68	88.03
Stephanodiscus niagarae Ehrenberg	*204*	1	.	7.30	30.50	327.25	10.85	59.18
Tabellaria binalis Ehrenberg	*205*	.	2	6.11	10.09	273.17	8.54	68.92
Tabellaria fenestrata (Lyngbye) Kützing	*206*	.	22	6.47	10.73	324.61	5.87	36.45
Tabellaria flocculosa 1 (Roth) Kützing	*207*	10	.	5.96	9.45	308.95	10.49	229.32
Tabellaria flocculosa 2 (Roth) Kützing	*208*	3	.	5.22	7.45	219.75	8.83	361.10
Tabellaria flocculosa 3 var.linearis Koppen	*209*	15	34	6.29	9.56	273.94	7.64	57.80
Tabellaria flocculosa 4 (Roth) Kützing	*210*	7	.	4.98	8.90	252.98	8.27	469.86
Tabellaria flocculosa small (Roth) Kützing	*211*	.	1	6.26	6.05	222.26	5.07	34.16
Tabellaria quadrisepta Knudson	*212*	.	9	6.29	11.83	342.87	8.21	53.10

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH	TP $\mu g.l^{-1}$	TN $\mu g.l^{-1}$	DOC $mg.l^{-1}$	CO_2 μM
Tabellaria ventricosa Kützing	*213*	23	.	5.79	8.00	234.76	8.79	304.21
Tabellaria ventricosa small Kützing	*214*		10	6.37	8.06	253.43	5.50	37.13

Appendix 2

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH optima	Hill's N2	% minimal	% maximal	Tolerance pH	type of species
Achnanthes 1 not identified	2	.	1	6.48	1	1	1	.	benthic
Achnanthes biasolettiana (Grunow) Cleve and Grunow	1	1	.	7.28	1	2.84	2.84	.	benthic
Achnanthes bioretii Germain	3	2	.	6.08	2	1.26	1.43	.	benthic
Achnanthes carissima (Lange-Bertalot) Lange-Bertalot and Krammer	4	.	1	6.71	1	1.17	1.17	.	benthic
Achnanthes catenata Bily and Marvan	5	2	.	6.00	1.8	1.2	2.44	.	benthic
Achnanthes flexella var. *alpestris* Brun	6	3	.	6.35	2.8	1	2	0.37	benthic
Achnanthes flexella var. *flexella* (Cleve) Cleve-Euler	7	1	.	7.80	1	1.2	1.2	.	benthic
Achnanthes joursacense Heribaud	8	1	.	6.75	1	2.33	2.33	.	benthic
Achnanthes kriegeri krasske	9	.	1	6.51	1	2.08	2.08	.	benthic
Achnanthes lanceolata var. *rostrata* (Oestrup) Lange-Bertalot	10	1	2	6.71	1.7	1.29	10.56	0.13	benthic
Achnanthes minutissima var. *affinis* (Lange-Bertalot) L.B. and K.	11	.	1	6.33	1	1.79	1.79	.	benthic
Achnanthes minutissima var. minutissima Kützing	12	24	17	6.72	19.6	1	26.95	0.99	benthic
*Achnanthes oblongell*a Oestrup	13	2	.	5.95	2	1.26	1.71	.	benthic
Achnanthes pusilla (Grunow) De Toni	14	3	.	7.04	2.5	1.27	4.96	0.26	benthic
Achnanthes ventralis (Krasske) Lange-Bertalot	15	4	.	7.45	1.9	1.11	9.59	0.58	benthic
Achnanthes ziegleri Lange-Bertalot	16	2	.	7.73	1.9	2.62	3.73	.	benthic
Actinella punctata Lewis	17	5	.	5.20	3.4	1.43	6.91	0.92	benthic
Amphicampa hemicyclus (Ehrenberg) Karsten	18	6	.	5.58	3.4	1.48	18.59	0.64	benthic
Amphipleura pellucida (Kützing) Kützing	19	1	.	7.28	1	1.65	1.65	.	benthic
Amphora ovalis (Kützing) Kützing	20	7	.	6.80	6.5	1	2.11	0.42	benthic
Amphora pediculus ver. *pediculus* (Kützing) Cleve	21	1	.	8.01	1	2.99	2.99	.	benthic
Amphora thumensis (Mayer) Cleve	22	1	.	8.01	1	1	1	.	benthic
Anomoeoneis aponina Kützing	23	.	2	5.91	1.7	1.1	2.53	.	benthic
Anomoeoneis I Brébisson	24	.	1	6.48	1	1.57	1.57	.	benthic
Anomoeoneis follis (Ehrenberg) Cleve	25	1	.	5.94	1	3.33	3.33	.	benthic
Anomoeoneis serians (Brébisson) Cleve	26	1	.	5.21	1	1.19	1.19	.	benthic
Anomoeoneis vitrea (Grunow) Ross	27	.	1	6.72	1	1.31	1.31	.	benthic
Asterionella formosa Hassall	28	12	29	6.08	12.9	1.05	49.08	0.74	benthic
Aulacoseira 1 not identified	29	3	.	5.70	2.5	1.29	5.25	0.37	planktonic
Aulacoseira 2 not identified	30	4	.	6.00	3.4	1.18	3.46	0.19	planktonic
Aulacoseira alpigena (Grunow) Krammer	31	.	17	6.47	9.7	1	18.56	0.41	planktonic
Aulacoseira ambigua (Grunow) Simonsen	32	11	.	6.47	4.1	1	33.52	1.07	planktonic
Aulacoseira distans var. *distans* (Ehrenberg) Simonsen	33	13	9	6.53	10.4	1	39.56	0.92	planktonic
Aulacoseira distans var. *humilis* Cleve-Euler	34	14	.	6.34	7.8	1.27	19.35	0.66	planktonic
Aulacoseira distans var. *nivalis* (W.Smith) Haworth	35	2	.	6.60	1.9	3.04	4.65	.	planktonic
Aulacoseira distans var. *nivaloides* Camburn	36	11	.	5.98	6.4	1	17.61	0.65	planktonic
Aulacoseira distans var. *tenella* (Nygaard) Florin	37	20	12	6.17	11.1	1	63.51	0.83	planktonic
Aulacoseira italica var. *subarctica* (O.Müller) Simonsen	38	6	32	6.51	20.6	1.84	44.42	0.40	planktonic
Aulacoseira italica var. *tenuissima* (Grunow) Simonsen	39	2	.	7.00	1.6	2.18	6.28	.	planktonic
Aulacoseira lacustris (Grunow) Krammer	40	1	.	4.18	1	4.85	4.85	.	planktonic
Aulacoseira lirata (Ehrenberg) Ross	41	10	15	6.20	14.6	1.48	46.68	0.67	planktonic
Aulacoseira lirata var. *biseriata* (Grunow) Haworth	42	2	.	5.49	1.5	1.41	4.95	.	planktonic
Aulacoseira nygaardii Camburn	43	5	.	5.33	4.5	1	3.27	0.98	planktonic
Aulacoseira pergiabra (Oestrup) Haworth	44	10	6	5.32	5.1	1	47.05	1.97	planktonic
Aulacoseira pergiabra var. *floriniae* Camburn	45	4	.	5.74	2	1.43	20.44	0.30	planktonic
Aulacoseira tenuior (Grunow)	46	4	1	5.89	4.4	1	2.52	0.48	planktonic
Brachysira brebissonii 1 not identified	47	19	13	6.07	17.7	1.08	15.96	0.51	planktonic
Brachysira brebissonii 3 not identified	48	1	.	5.94	1	7.1	7.1	.	benthic
Brachysira procera Lange-Bertalot	49	2	.	6.30	1.9	1.18	1.77	.	benthic
Brachysira styriaca (Grunow) Hustedt	50	2	.	6.46	1.8	1.29	2.66	.	benthic
Brachysira vitrea (Grunow) Ross	51	14	.	6.78	6.8	1	19.59	0.95	benthic
Caloneis silicula (Ehrenberg) Cleve	52	.	1	6.54	1	1.32	1.32	.	benthic
Cocconeis placentula var. *euglypta* Ehrenberg	53	1	.	7.40	1	1	1	.	benthic
Cyclotella antiqua W. Smith	54	1	.	7.40	1	1.46	1.46	.	benthic
*Cyclotella bodanic*a Grunow	55	2	.	6.89	1.6	2.96	8.37	.	planktonic
Cyclotella bodanica var. *lemanica* (O.Müller) Bachmann	56	11	25	6.63	18	1.28	39.32	0.52	planktonic

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH optima	Hill's N2	% minimal	% maximal	Tolerance pH	type of species
Cyclotella comensis Grunow	57	.	8	6.39	5.9	1.49	9.4	0.41	planktonic
Cyclotella distinguenda Hustedt	58	.	1	6.28	1	1	1	.	planktonic
Cyclotella gamma Skvortow	59	1	.	7.80	1	1	1	.	planktonic
Cyclotella glomerata Bachmann	60	.	3	6.43	1.2	1.44	41.02	0.06	planktonic
Cyclotella meneghiniana Kützing	61	4	1	6.69	3.6	1	4.52	0.57	planktonic
Cyclotella michiganiana Skvortzow	62	7	.	7.08	4.6	1	11.75	0.69	planktonic
Cyclotella ocellata Pantocsek	63	5	6	6.73	6.4	1	6.86	0.32	planktonic
Cyclotella pseudostelligera 1 not identified	64	7	1	6.32	6	1.11	11.09	0.75	planktonic
Cyclotella pseudostelligera 3 not identified	65	5	.	7.06	3.2	1.08	10.47	0.46	planktonic
Cyclotella rossii Håkansson	66	.	3	6.74	2.4	2.09	5.86	0.03	planktonic
Cyclotella stelligera 1 not identified	67	13	25	6.49	21.8	1	34.24	0.56	planktonic
Cyclotella stelligera 3 not identified	68	1	.	6.12	1	5.56	5.56	.	planktonic
Cyclotella stelligeroides Hustedt	69	2	.	6.26	1.3	4.86	28.5	.	planktonic
Cymbella aequalis W. Smith	70	1	.	6.95	1	4.66	4.66	.	planktonic
Cymbella cesatii (Rabenhorst) Grunow	71	1	.	7.57	1	1.13	1.13	.	benthic
Cymbella delicatula Kützing	72	2	.	7.58	1.1	1.2	21.85	.	benthic
Cymbella gaeumannii Meister	73	10	.	5.62	7.5	1	3.95	0.62	benthic
Cymbella gracilis (Ehrenberg) Kützing	74	6	3	6.17	8.7	1	1.88	0.53	benthic
Cymbella hebridica (Grunow) Cleve	75	8	1	5.18	3	1	16.46	1.07	benthic
Cymbella incerta (Grunow) Cleve	76	5	.	6.39	4.5	1.2	3.33	0.44	benthic
Cymbella microcephala Grunow	77	7	1	6.53	4.9	1	7.8	1.47	benthic
Cymbella minuta Hilse	78	1	.	4.54	1	1.24	1.24	.	benthic
Cymbella naviculiformis Auerswald	79	1	.	6.59	1	1.01	1.01	.	benthic
Cymbella silesiaca Bleisch	80	4	5	8.31	4.1	1	9.14	0.46	benthic
Denticula elegans Kützing	81	3	.	7.30	2.4	3.84	17.52	0.36	benthic
Diploneis elliptica (Kützing) Cleve	82	.	1	6.71	1	1.17	1.17	.	benthic
Diploneis modica Hustedt	83	3	.	6.59	2.9	1.05	1.65	0.29	benthic
Diploneis ovalis (Hilse) Cleve	84	3	.	7.16	2.7	1	2.33	0.11	benthic
Diploneis puella (Schumann)	85	2	.	6.74	1.8	1.08	2.1	.	benthic
Eunotia arculus (Grunow) Lange-Bertalot	86	.	1	5.90	1	1.36	1.36	.	benthic
Eunotia arcus Ehrenberg	87	1	.	6.95	1	1.55	1.55	.	benthic
Eunotia bidentula Schumann	88	7	.	4.66	6.3	1	3.22	0.36	benthic
Eunotia bilunaris (Ehrenberg) Mills	89	10	.	5.20	4.9	1.05	17.04	0.96	benthic
Eunotia bilunaris var. *mucophyla* Lange-Bertalot and Nörpel	90	6	12	6.01	15.6	1	2.49	0.69	benthic
Eunotia carolina Patrick	91	1	.	5.21	1	1.9	1.9	.	benthic
Eunotia elegans Oestrup	92	.	1	6.33	1	1	1	.	benthic
Eunotia exigua (Brébisson) Rabenhorst	93	5	2	5.93	5.4	1	2.38	0.86	benthic
Eunotia exigua var. *bidens* Hustedt	94	.	2	6.36	2	1	1.11	.	benthic
Eunotia faba Ehrenberg	95	2	4	5.85	3.7	1.12	4.47	0.94	benthic
Eunotia flexuosa (Brébisson) (Kützing)	96	1	1	6.65	2	1	1	.	benthic
Eunotia glacialis Meister	97	.	2	6.63	1.9	1.05	1.75	.	benthic
Eunotia hemicyclus (Ehrenberg) Ralfs	98	.	1	6.34	1	1	1	.	benthic
Eunotia implicata Nörpel et al.	99	2	.	6.56	1.9	1.05	1.46	.	benthic
Eunotia incisa Gregory	100	7	13	6.14	14.9	1	5.38	0.48	benthic
Eunotia linearis Okuno	101	.	4	6.31	3.6	1	1.7	0.21	benthic
Eunotia meisteri Hustedt	102	1	1	6.68	1.9	1.11	1.85	.	benthic
Eunotia microcephala Krasske	103	2	.	5.86	2	1.48	2.47	.	benthic
Eunotia minor (Kützing) Grunow	104	1	2	5.38	2.7	1	1.98	0.86	benthic
Eunotia naegelii Migula	105	.	1	6.40	1	1.63	1.63	.	benthic
Eunotia nymanniana Grunow	106	2	.	5.15	1.9	1	1.48	.	benthic
Eunotia paludosa Grunow	107	5	2	6.43	3.7	1	7.88	0.73	benthic
Eunotia pectinalis (Dillwyn) Rabenhorst	108	.	9	8.38	7.3	1.08	3.5	0.35	benthic
Eunotia pectinalis var. *ventralis* (Ehrenberg) Hustedt	109	7	.	5.18	3.7	1	13.37	0.90	benthic
Eunotia pirla Carter	110	4	.	4.73	3.6	1	2.72	0.35	benthic
Eunotia polyglyphis Grunow	111	5	.	6.67	2.5	1	7.06	1.19	benthic
Eunotia praerupta Ehrenberg	112	2	.	7.05	1.4	1	5.32	.	benthic

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH optima	Hill's N2	% minimal	% maximal	Tolerance pH	type of species
Eunotia pyramidata Hustedt	*113*	.	2	5.98	2	1	1.28	.	benthic
Eunotia rhomboidea Hustedt	*114*	8	.	4.84	5.3	1.11	6.68	0.40	benthic
Eunotia rhynchocephala Krasske	*115*	4	.	5.64	4	1	1.29	0.38	benthic
Eunotia schwabei Krasske	*116*	.	3	6.37	2.9	1	1.42	0.26	benthic
Eunotia seminulum (Nörpel) Lange-Bertalot	*117*	.	1	6.61	1	1.28	1.28	.	benthic
Eunotia septentrionalis Oestrup	*118*	2	.	5.34	1.9	1.17	1.9	.	benthic
Eunotia serra Ehrenberg	*119*	3	1	5.60	3.6	1	2.06	1.13	benthic
Eunotia serra var. *diadema* (Ehrenberg) Patrick	*120*	.	1	6.22	1	1.48	1.48	.	benthic
Eunotia subarcuatoides Alles et al.	*121*	1	5	5.99	6	1.23	1.52	0.65	benthic
Eunotia sudetica O.Müller	*122*	2	.	4.95	1.9	1.4	2	.	benthic
Eunotia tenera W. Smith	*123*	16	.	6.74	9.9	1	16.09	0.61	benthic
Fragilaria brevistriata 1 not identified	*124*	7	.	6.73	4.9	1.91	13.89	0.78	benthic
Fragilaria brevistriata 2 not identified	*125*	2	.	7.96	1.6	4.56	15.17	.	benthic
Fragilaria brevistriata 3 Grunow	*126*	4	5	6.67	6.1	1	6.87	0.16	benthic
Fragilaria capucina Desmazières	*127*	4	.	5.44	3.2	1.26	4.44	0.67	benthic
Fragilaria constricta Ehrenberg	*128*	4	.	4.99	3	2.54	11.11	0.31	benthic
Fragilaria constricta var. *stricta* Cleve	*129*	1	2	6.60	2.8	1.26	2.71	0.24	benthic
Fragilaria construens var. *binodis* (Ehrenberg) Grunow	*130*	13	4	6.89	8.8	1	17.88	0.86	benthic
Fragilaria construens var. *construens* (Ehrenberg) Grunow	*131*	1	1	7.04	1	1.91	1.91	1.06	benthic
Fragilaria construens var. *spiranum* (Ehrenberg) Grunow	*132*	.	1	6.74	1.4	1.95	8.47	.	benthic
Fragilaria construens var. *venter* (Ehrenberg) Grunow	*133*	3	11	6.27	7.7	1	21.64	.	benthic
Fragilaria crotonensis Kitton	*134*	.	1	6.40	1	3.18	3.18	.	planktonic
Fragilaria exigua Grunow	*135*	.	1	6.74	1	2.49	2.49	.	benthic
Fragilaria fasciculata (Agardh) Lange-Bertalot	*136*	4	2	5.73	5.2	0.84	2.37	0.76	benthic
Fragilaria inflata Pantocsek	*137*	1	.	5.44	1	1.51	1.51	.	benthic
Fragilaria inflata var. *istranii* Pantocsek	*138*	1	.	7.30	1	2.22	2.22	.	benthic
Fragilaria intermedia Grunow	*139*	5	.	7.24	3.1	1.23	7.86	0.36	benthic
Fragilaria lapponica Grunow	*140*	1	.	5.39	1	2.94	2.94	.	benthic
Fragilaria lata (Cleve-Euler) Renberg	*141*	9	.	6.65	7.2	1	4.38	1.16	benthic
Fragilaria nenana Lange-Bertalot	*142*	5	.	6.41	4.3	2.38	6.05	0.81	benthic
Fragilaria pinnata Ehrenberg	*143*	.	2	6.69	3.5	1.68	39.99	.	benthic
Fragilaria pinnata var. *pinata* Ehrenberg	*144*	10	.	7.19	2	1	1.1	0.46	benthic
Fragilaria pseudoconstruens Marciniak	*145*	.	1	6.44	1	1.03	1.03	.	benthic
Fragilaria vaucheriae (Kützing) Petersen	*146*	.	1	6.51	1	10.57	10.57	.	benthic
Fragilaria virescens var. *exigua* Grunow	*147*	15	.	5.90	7.6	1.44	38.15	0.59	benthic
Fragilaria 1 not identified	*148*	.	1	6.28	1	1	1	.	benthic
Frustulia rhomboides 1 not identified	*149*	.	2	6.16	16.1	1	13.57	.	benthic
Frustulia rhomboides 3 not identified	*150*	.	24	6.28	1.8	1.26	2.32	0.35	benthic
Frustulia rhomboides var. *amphipleuroides* (Grunow) De Toni	*151*	1	.	4.60	1	1.23	1.23	.	benthic
Frustulia rhomboides var. *crassinervia* (Brébisson) Ross	*152*	24	.	5.47	2	1.3	1.36	1.02	benthic
Frustulia rhomboides var. *saxonica* (Rabenhorst) De Toni	*153*	2	.	4.59	17.6	1	7.14	.	benthic
Gomphonema 1 not identified	*154*	1	.	6.80	1	1.17	1.17	.	benthic
Gomphonema angustatum Agardh	*155*	.	2	6.37	1.9	1	1.73	.	benthic
Gomphonema gracile Ehrenberg	*156*	4	3	6.77	6.7	1	2.05	0.61	benthic
Gomphonema parvulum (Kützing) Kützing	*157*	2	.	6.67	2	1.46	1.63	.	benthic
Gomphonema subtile Ehrenberg	*158*	2	.	6.93	1.6	1.11	3.1	.	benthic
Navicula 1 not identified	*159*	4	.	7.46	3.4	1	4.08	0.37	benthic
Navicula 2 not identified	*160*	3	.	6.73	2.7	1	2.13	0.58	benthic
Navicula brachysira Brébisson	*161*	4	.	5.86	3.5	1.01	2.82	0.43	benthic
Navicula bulnheimii Grunow	*162*	.	1	6.95	1	1.44	1.44	.	benthic
Navicula cocconeiformis Gregory	*163*	3	.	6.57	2.8	1	1.61	0.63	benthic
Navicula cryptocephala Kützing	*164*	2	.	7.31	1.7	1	2.6	.	benthic
Navicula cryptotenelle Lange-Bertalot	*165*	4	.	7.31	3.2	1	4.26	0.23	benthic
Navicula diluviana Krasske	*166*	2	.	7.95	1.7	5.28	13.18	.	benthic
Navicula indifferens Hustedt	*167*	.	1	6.40	1	1.41	1.41	.	benthic
Navicula kuelbsii Lange-Bertalot	*168*	.	1	6.71	1	1.56	1.56	.	benthic

Diatom flora description	species number	occurrence Abitibi	occurrence Gouin	pH optima	Hill's N2	% minimal	% maximal	Tolerance pH	type of species
Navicula laevissima Kützing	169	9	.	6.45	7.1	1.2	4.88	0.90	benthic
Navicula leptostriata Jørgensen	170	4	.	6.10	3.9	1.05	1.55	0.88	benthic
Navicula mediocris Krasske	171	5	.	6.12	4.7	1.05	2	0.41	benthic
Navicula molestiformis Hustedt	172	.	3	6.24	2.8	1.4	2.61	0.28	benthic
Navicula pupula Kützing	173	9	1	6.73	9	1	3.1	0.61	benthic
Navicula radiosa Kützing	174	7	4	6.71	8.2	1	4.96	0.63	benthic
Navicula scutiformis Grunow	175	.	1	6.43	1	1.09	1.09	.	benthic
Navicula seminuloides Grunow	176	3	.	6.37	2.9	1.05	1.65	0.75	benthic
Navicula seminulum Grunow	177	1	.	6.09	1	1.26	1.26	.	benthic
Navicula soehrensis var. *muscicola* (Petersen) Krasske	178	.	1	6.43	1	1.82	1.82	.	benthic
Navicula stroemii Hustedt	179	1	.	7.30	1	1.48	1.48	.	benthic
Navicula subatomoides Hustedt	180	6	3	6.50	8.1	1	2.43	0.84	benthic
Navicula subtilissima Cleve	181	9	2	5.40	1.8	1.08	53.57	0.52	benthic
Navicula viridula (Kützing) A94	182	1	.	7.80	1	1.68	1.68	.	benthic
Neidium ampliatum (Ehrenberg) Krammer	183	10	1	5.09	7.8	1	5.56	0.74	benthic
Neidium iridis (Ehrenberg) Cleve	184	9	.	5.04	3.3	1.05	11.52	1.02	benthic
Nitzschia minutula Grunow	185	11	.	6.46	7.4	1.06	7.08	0.68	benthic
Nitzschia fonticola Grunow	186	7	1	6.35	6.1	1	5.13	1.19	benthic
Pinnularia 1 not identified	187	3	.	4.91	2.5	2.26	7.38	0.34	benthic
Pinnularia biceps Gregory	188	.	1	6.40	1	2.24	2.24	.	benthic
Pinnularia braunii (Grunow) Cleve	189	14	.	5.30	5.2	1	24.75	1.34	benthic
Pinnularia divergens W. Smith	190	.	2	6.52	1.4	1.03	4.72	.	benthic
Pinnularia gibba Ehrenberg	191	12	1	5.81	9.4	1	6.42	1.02	benthic
Pinnularia interrupta W. Smith	192	3	.	6.00	2.6	1	3.32	0.93	benthic
Pinnularia maior (Kützing) Rabenhorst	193	5	3	6.50	7.8	1	1.55	0.58	benthic
Pinnularia mesolepta (Ehrenberg) W. Smith	194	.	1	6.54	1	6.98	6.98	.	benthic
Pinnularia microstauron 1 Ehrenberg	195	5	1	5.84	5.2	1	2.67	1.15	benthic
Pinnularia microstauron 2 Ehrenberg	196	11	.	5.63	10	1	2.88	0.77	benthic
Pinnularia schoenfelderii Krammer	197	.	3	6.54	1.7	1.24	8.3	0.06	benthic
Pinnularia viridis (Nitzsch) Ehrenberg	198	4	.	5.24	3.2	1.01	3.5	1.03	benthic
Stauroneis agrestis Petersen	199	6	.	5.70	5.4	1	2.4	1.03	benthic
Stauroneis anceps Ehrenberg	200	.	2	6.58	1.9	2.5	3.49	.	benthic
Steuroneis gracilis Ehrenberg	201	.	1	6.54	1	3.21	3.21	1.13	benthic
Stauroneis phoenicenteron (Nitzsch) Ehrenberg	202	9	1	6.04	8	1	3.44	.	benthic
Stauroneis producta Grunow	203	.	1	5.90	1	1.8	1.8	.	benthic
Stephanodiscus niagarae Ehrenberg	204	1	.	7.30	1	2.59	2.59	.	benthic
Tabellaria binalis Ehrenberg	205	.	2	6.11	2	1	1.03	0.32	planktonic
Tabellaria fenestrata (Lyngbye) Kützing	206	.	22	6.47	11.2	1	15.96	0.70	planktonic
Tabellaria flocculosa 1 (Roth) Kützing	207	10	.	5.96	7.9	1	3.52	0.29	planktonic
Tabellaria flocculosa 2 (Roth) Kützing	208	3	.	5.22	2.1	1	4.2	0.54	planktonic
Tabellaria flocculosa 3 var.linearis Koppen	209	15	34	6.29	20.9	1	46.82	0.30	planktonic
Tabellaria flocculosa 4 (Roth) Kützing	210	7	.	4.98	5.9	1	3.21	.	planktonic
Tabellaria flocculosa small (Roth) Kützing	211	.	1	6.26	1	33.4	33.4	0.33	planktonic
Tabellaria quadrisepta Knudson	212	.	9	6.29	6.7	1	3.71	0.93	planktonic
Tabellaria ventricosa Kützing	213	23	.	5.79	5.4	1.07	9.54	0.15	planktonic
Tabellaria ventricosa small Kützing	214		10	6.37	13.8	1	9.88	.	planktonic

Appendix 3

Diatom flora description	species number	occurrence	pH	TP (µg.l^{-1})	TN(µg.l^{-1})	color (mg/Pt)	CO_2 (µM)
Achnanthes acares Hohn & Hellermann	1	1	6.50	34.00	688.00	180.00	50.39
Achnanthes curtissima Carter	2	1	4.90	43.60	718.08	118.00	2429.00
Achnanthes delicatissima Simonsen	3	2	6.48	33.83	663.54	1789.97	97.00
Achnanthes exigua Grunow	4	6	6.79	35.29	684.41	1310.31	106.80
Achnanthes impexa Lange-Bertalot	5	2	6.57	71.74	815.75	1731.49	84.94
Achnanthes intermedia Kützing	6	1	6.80	125.00	1086.00	225.00	27.26
Achnanthes lanceolata (Brébisson) Grunow	7	6	7.01	33.67	999.66	152.18	116.87
Achnanthes lanceolata var. *frequentissima* Lange-Bertalot	8	6	7.19	45.88	835.78	236.23	78.29
Achnanthes laterostrata Hustedt	9	3	6.86	51.69	821.93	277.76	175.65
Achnanthes marginulata Grunow	10	6	6.63	42.87	641.53	1164.93	95.68
Achnanthes minutissima Kützing	11	33	6.76	42.57	888.05	151.88	465.46
Achnanthes minutissima var. *affinis* (Lange-Bertalot) L.B. and K.	12	7	7.05	40.01	1051.07	128.99	40.36
Achnanthes minutissima var. *jackii* (Rabenhorst) Lange-Bertalot	13	2	6.83	42.55	904.00	326.40	368.46
Achnanthes minutissima var. *saprophila* I Kobayasi & Mayama	14	3	6.78	66.32	1357.20	171.67	213.83
Achnanthes minutissima var. *saprophila* II Kobayasi & Mayama	15	3	6.99	35.18	655.21	296.24	104.43
Achanthes oestrupii (Cleve-Euker)	16	2	6.39	51.02	693.34	244.40	601.39
Achnanthes rosenstockii Lange-Bertalot	17	5	6.50	34.00	688.00	180.00	50.39
Achnanthes seccula Carter	18	1	6.69	37.83	655.28	1029.44	105.71
Achnanthes suchlandtii Hustedt	19	9	8.00	28.70	786.47	18.47	36.54
Amphora inariensis (Krammer)	20	1	7.41	64.65	1277.32	63.16	120.53
Amphora lybica Ehrenberg	21	6	7.88	37.70	930.66	65.15	28.73
Amphora ovalis var. *pediculus* (Kützing) Cleve	22	6	8.00	44.20	1691.23	31.00	20.92
Anomoeoneis vitrea (Grunow) Ross	23	1	6.67	67.61	899.47	235.45	279.47
Asterionella formosa Hassall	24	19	6.60	78.55	572.87	313.07	82.16
Aulacoseira alpigena (Grunow) Krammer	25	2	7.70	14.00	510.00	152.00	19.71
Aulacoseira lirata (Ehrenberg) Ross	26	1	6.60	79.00	552.00	312.00	79.83
Aulacoseira italica var. *subarctica* (O.Müller) Simonsen	27	26	7.07	53.66	820.06	199.37	87.80
Aulacoseira sp. Thwaites	28	1	7.94	48.01	1289.47	61.81	64.07
Cocconeis placentula var. *euglypta* Ehrenberg	29	15	7.47	29.96	826.54	38.89	18.97
Cocconeis placentula var. *placentula* Ehrenberg	30	5	7.74	51.04	1058.73	119.99	73.52
Cyclotella bodanica var. *lemanica* (O.Müller) Bachmann	31	11	6.75	27.87	905.37	45.54	50.53
Cyclotella distinguenda Hustedt	32	2	6.56	49.35	818.19	357.08	390.23
Cyclotella glomerata Bachmann	33	8	7.66	101.89	1724.82	68.78	80.74
Cyclotella meneghiniana Kützing	34	5	7.76	29.91	1017.78	36.60	47.53
Cyclotella ocellata Pantocsek	35	1	8.20	16.00	540.00	.	30.37
Cyclotella stelligera Cleve & Grunow	36	4	6.86	45.78	975.14	202.76	186.29
Cymbella cistula (Ehrenberg) Kirchner	37	2	7.98	39.68	1104.61	48.44	55.87
Cymbella minuta Hilse	38	3	7.01	33.75	919.62	131.84	188.73
Epithemia turgida (Ehrenberg) Kützing	39	4	7.91	35.01	1322.37	40.53	62.17
Eunotia bilunaris (Ehrenberg) Mills	40	2	6.00	38.70	661.32	241.09	1024.65
Eunotia incisa Gregory	41	2	5.05	34.52	790.66	93.01	2467.67
Eunotia sp. Ehrenberg	42	2	5.55	36.75	669.91	125.87	1871.29
Fragilaria berolinensis I (Lemmermann)	43	1	7.60	29.10	709.66	59.67	60.80
Fragilaria berolinensis II (Lemmermann)	44	3	6.33	82.92	1758.35	268.49	272.55
Fragilaria brevistriata Grunow	45	25	6.93	50.49	907.52	245.47	123.48
Fragilaria construens (Ehrenberg) Grunow	46	8	7.05	33.40	1213.09	73.32	255.40
Fragilaria construens var. *binodis* (Ehrenberg) Grunow	47	2	7.68	29.64	1337.29	40.77	86.06
Fragilaria construens var. *vantar* (Ehrenberg) Grunow	48	31	6.76	52.80	1005.18	172.09	350.82
Fragilaria crotonensis Kitton	49	9	7.45	40.23	843.36	71.76	48.38
Fragilaria intermedia Grunow	50	1	6.90	109.00	718.00	448.00	95.36
Fragilaria lapponica Grunow	51	5	7.22	48.38	1274.91	168.02	81.21
Fragilaria leptostauron (Ehrenberg)	52	1	8.00	28.70	786.47	18.47	36.54
Fragilaria parasitica (W. Smith) Grunow	53	2	6.51	34.71	680.51	1449.63	87.02
Fragilaria pinnata var. *pinata* Ehrenberg	54	30	6.89	43.81	819.74	257.59	95.41
Fragilaria tenera (W. Smith)	55	3	6.67	65.57	1554.89	217.99	248.27
Frustulia rhomboides var. *saxonica* (Rabenhorst) De Toni	56	2	5.74	28.14	747.28	1335.75	1435.74
Gomphonema acuminatum var. *turis* (Ehrenberg)	57	5	7.41	31.44	949.01	50.13	45.36
Gomphonema angustatum Agardh	58	4	7.36	34.66	991.81	499.35	74.19

Diatom flora description	species number	occurrence	pH	TP (µg.l^{-1})	TN(µg.l^{-1})	color (mg/Pt)	CO_2 (µM)
Gomphonema minutum (Agardh) Agardh	59	4	7.61	32.55	881.30	32.44	21.37
Gyrosigma acuminatum (Kützing) Rabenhorst	60	3	8.37	42.28	1031.56	47.13	13.82
Navicula cryptocephala Kützing	61	5	6.15	44.36	1068.90	143.89	973.55
Navicula cryptotenella Lange-Bertalot	62	8	7.08	32.20	1049.11	85.40	283.50
Navicula difficillima Hustedt	63	11	7.04	42.53	1251.06	61.70	185.42
Navicula indifferens Hustedt	64	11	6.40	51.99	867.44	171.01	707.36
Navicula kuelbsii Lange-Bertalot	65	7	6.18	44.56	748.91	722.77	767.16
Navicula laevissima Kützing	66	2	5.58	46.13	793.00	158.02	1464.54
Navicula leptostriata Jørgensen	67	1	6.80	50.18	1060.57	97.13	167.22
Navicula molestiformis Hustedt	68	5	7.10	30.20	1238.41	45.00	148.06
Navicula polyonca Brébisson	69	2	6.91	35.31	849.23	1492.18	99.50
Navicula pupula Kützing	70	15	6.77	87.09	1044.46	408.00	133.16
Navicula radiosa Kützing	71	4	7.09	41.63	1067.23	98.67	253.36
Navicula scutiformis Grunow	72	1	7.07	28.02	1070.22	55.86	158.06
Navicula subatomoides Hustedt	73	6	8.00	28.70	786.47	18.47	36.54
Navicula subtilissima Cleve	74	1	6.48	41.61	636.53	1517.81	131.50
Neidium ampliatum (Ehrenberg) Krammer	75	2	7.10	30.20	1238.41	45.00	148.06
Opephora olsenii Möller	76	2	5.84	27.29	988.30	60.88	1707.43
Pinnularia gibba Ehrenberg	77	4	7.36	21.75	659.15	45.77	19.49
Pinnularia interrupta W. Smith	78	4	6.73	31.56	1049.57	102.49	381.32
Pinnularia lundii Hustedt	79	1	6.69	58.70	1194.41	162.65	207.59
Pinnularia nobilis Ehrenberg	80	1	5.20	25.80	860.41	69.00	2504.84
Pinnularia nodosa Ehrenberg	81	2	6.50	40.00	612.00	484.00	139.06
Pinnularia viridis (Nitzsch) Ehrenberg	82	6	8.24	145.22	2573.23	94.44	19.45
Rhopalodia gibba (Ehrenberg) O.Müller	83	1	6.63	60.42	1272.10	173.00	814.06
Stauroneis anceps Ehrenberg	84	3	8.00	44.20	1691.23	31.00	20.92
Stauroneis phoenicenteron (Nitzsch) Ehrenberg	85	4	5.77	41.35	777.05	170.51	1624.74
Stephanodiscus hantschii Grunow	86	10	7.71	32.24	1140.38	43.02	77.43
Stephanodiscus niagarae Ehrenberg	87	6	7.80	29.05	729.22	184.70	62.34
Synedra ulna Ehrenberg	88	3	7.66	28.74	897.71	32.79	21.51
Tabellaria fenestrata (Lyngbye) Kützing	89	1	7.70	14.00	510.00	152.00	19.71
Tabellaria flocculosa (Roth) Kützing	90	18	6.77	49.63	805.70	182.44	330.29

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A comparison between diatom-based pH inference models using Artificial Neural Networks (ANN), Weighted Averaging (WA) and Weighted Averaging Partial Least Squares (WA-PLS) regressions

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Abstract

We explored the possibility of using artificial neural networks (ANN) to develop quantitative inference models in paleolimnology. ANNs are dynamic computer systems able to learn the relations between input and output data. We developed ANN models to infer pH from fossil diatom assemblages using a calibration data set of 76 lakes in Quebec. We evaluated the predictive power of these models in comparison with the two most commonly methods used in paleolimnology: Weighted Averaging (WA) and Weighted Averaging Partial Least Squares (WA-PLS). Results show that the relationship between species assemblages and environmental variables of interest can be modelled by a 3-layer back-propagation network, with apparent R^2 and RMSE of 0.9 and 0.24 pH units, respectively. Leave-one-out cross-validation was used to access the reliabilities of the WA, WA-PLS and ANN models. Validation results show that the ANN model ($R^2_{jackknife} = 0.63$, $RMSE_{jackknife} = 0.45$, mean bias = 0.14, maximum bias = 1.13) gives a better predictive power than the WA model ($R^2_{jackknife} = 0.56$, $RMSE_{jackknife} = 0.5$, mean bias = –0.09, maximum bias = –1.07) or WA-PLS model ($R^2_{jackknife} = 0.58$, $RMSE_{jackknife} = 0.48$, mean bias = –0.15, maximum bias = –1.08). We also evaluated whether the removal of certain taxa according to their tolerance changed the performance of the models. Overall, we found that the removal of taxa with high tolerances for pH improved the predictive power of WA-PLS models whereas the removal of low tolerance taxa lowered its performance. However, ANN models were generally much less affected by the removal of taxa of either low or high pH tolerance. Moreover, the best model was obtained by averaging the predictions of WA-PLS and ANN models. This implies that the two modelling approaches capture and extract complementary information from diatom assemblages. We suggest that future modelling efforts might achieve better results using analogous multi-model strategies.

Introduction

The first quantitative paleoenvironmental reconstruction models developed by Imbrie and Kipp (1973) were based on linear or curvilinear regression models between principal components extracted from modern species assemblages and environmental variables of interest. Since then, several other models have been proposed, two of which are now widely used in paleolimnology: Weighted Averaging regression (WA) (ter Braak & van Dam, 1989; Birks et al., 1990) and Weighted Averaging-Partial Least-Squares regression (WA-PLS) (ter Braak & Juggins, 1993). These models assume a unimodal relationship between species and environmental variables. However, even though it is usual in a calibration data set that some taxa show a statistically significant unimodal or linear response to the environmental gradient of interest, other taxa may show a skewed unimodal or sigmoid increasing or decreasing response (Huisman et al., 1993; Birks, 1998). Therefore, models with a sufficient flexibility to accommodate the full range of observed responses might

be more powerful than methods that assume either a unimodal response of all taxa or a linear response of all taxa (Birks, 1998).

Artificial neural networks (ANN) have the potential for modelling and incorporating such mixtures of responses. Derived from Artificial Intelligence (AI), ANNs are dynamic computer systems capable of 'learning' the relations between input and output data. They are composed of many non-linearly inter-connected simple processing units (neurons) that work in parallel. During the training process (iterative simulations), the network adapts itself from examples and the optimal relations (functions) between the input and output data are found and implemented automatically. The implemented function can then be used to predict dependent variables using only the independent ones. The main advantage in using ANN is that no *a priori* assumptions about the relation between inputs (independent variables) and output (dependent variable) are necessary. However, the drawback is that those relations learned by an ANN are hidden in its neural architecture and cannot be expressed in traditional mathematical terms.

ANNs are used in various fields including physics (Rahim et al., 1993) and medicine (Lerner et al., 1994). In ecology they are seldom used, although a few papers have shown that they can give superior results to more traditional statistical methods such as multiple regression (Brey et al., 1996; Lek et al., 1996; Moatar et al., 1999). Comparisons have also been made to paleoceanographic tools like MAT (Modern Analog Technique) (Malmgren & Nordlund, 1997), Imbrie and Kipp-type transfer functions (Malmgren & Nordlund, 1997) and SIMCA (Soft Independent Modelling of Class Analogy) (Malmgren & Nordlund, 1997).

In this paper, we propose a modelling method based on one form of neural networks: the back-propagation algorithm (Rumelhart et al., 1986). We explore the potential of this approach to modelling and inferring pH from a diatom calibration data set based on 76 lakes in Quebec. We then compare the ANN results to two other techniques commonly used in paleolimnology: WA and WA-PLS.

Methods

ANN principle

Artificial neuron

An artificial neuron is a processing element like a biological neuron (Figure 1a). It works as follows: (1) it receives input (from the original data or from the output of other neurons in the network). Each input comes via a connection which has a given strength (weight); these weights correspond to the synaptic efficiency in a biological neuron. The weighted sum of the inputs is formed to compose the activation of the neuron. (2) The activation signal is passed through an activation function (sigmoid, tan sigmoid, linear or step function) to produce the output of the neuron. The output is then duplicated as many times as needed.

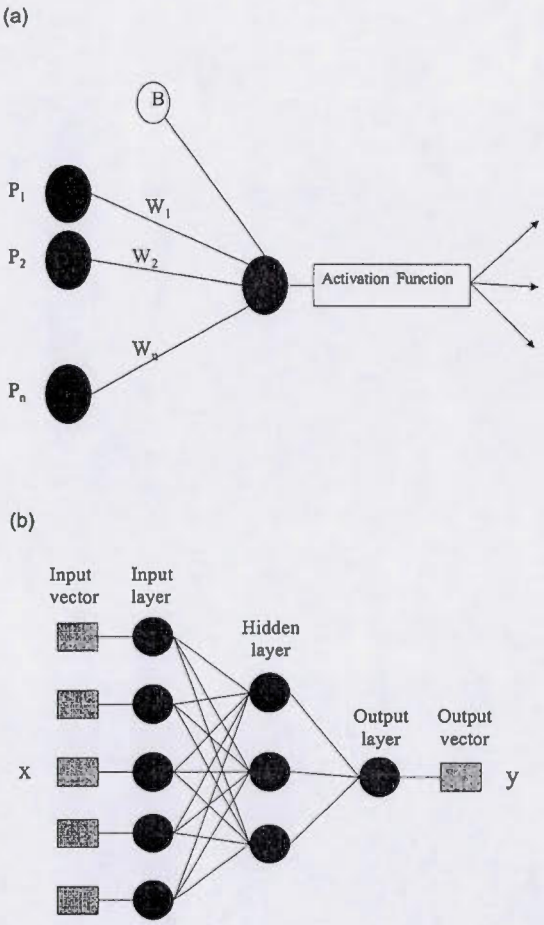

Figure 1. (a) Schematic representation of a simple processing element. The incoming signals (p) are multiplied by the weight of the connections (W) and summed. The bias (B) is then added, and the resulting sum is filtered through the activation function to produce the activity of the neuron. (b) Schematic representation of the general architecture of a 3-layer back-propagation network with five elements in the input layer, three neurons in the hidden layer, and one neuron in the output layer.

Back-propagation neural networks

In this type of network, neurons are arranged in a distinct layered topology: one input layer, one or more hidden layers and one output layer (Figure 1b). The input layer is not really neural at all: these units simply serve to introduce the value of the input variables. The hidden and output layer neurons are each connected to all of the units in the preceeding layer.

The back-propagation algorithm (descending gradient algorithm) is based on supervised learning, namely to learn, the system has to know, for each example, the output (environmental variable) associated with the input (species data). The learning phase consists of adjusting the weights of the network connections by feeding a set of input/target pattern pairs (examples) many times. The back-propagation algorithm works as follows: (1) the network is initialised by assigning a learning rate, a maximum number of iterations and random values to the synaptic weights; (2) a training pattern is fed and propagated forward through the network to compute an output value for each output unit; (3) the computed output is compared with the expected output; (4) a backward pass through the network is performed, changing the synaptic weight on the basis of the observed output errors. Steps 2 through 4 are iterated for each pattern in a training set, then the network performance is checked and a new set of training patterns is submitted to the network (i.e., a new epoch is started) if it needs further optimization. This dynamic procedure allows the difference between the predicted output and observed output to converge towards a minimal value. Details of the back-propagation algorithm are presented in Appendix 1.

Back-propagation networks are also called 'universal approximators' and, as such, they are ultimately able to learn any pattern perfectly. These networks are only really useful if they are capable, after a learning period, of generalizing. In order to generalize, a network must be able to produce the correct output data on samples not included in the learning set. A well-built neural network will, after training with a learning set, give a high proportion of correct predictions when fed a validation set. Background information on ANNs is available in various introductory textbooks such as Bishop (1995).

Data set

Data for 76 lakes distributed in two regions of Quebec (Abitibi and Réservoir Gouin) were used in this study. Lakes in Réservoir Gouin (n = 35) were sampled three times during the ice-free season in 1996 and 1997 while the Abitibi lakes (n = 41) were sampled twice between June and August 1996 (n = 20) and 1997 (n = 21) (for details, see Enache & Prairie, in press). pH values are summer averages obtained from these samples. The range, mean and median are summarised in Table 1.

Modern diatoms recovered from the surface sediments of the 76 lakes were processed, identified and counted (for methodological details, see Enache & Prairie, in press). In total, 214 fossil diatom taxa (relative abundance > 1%) were identified. Only 20% of the 214 taxa are present in at least 10 lakes while 50% are present in 3 lakes or less. An average of 18 taxa were identified per lake. Some details of the species data-set are summarised in Table 1.

Numerical methods

We determined whether to use linear- or unimodal-based regression and calibration techniques (ter Braak & Prentice, 1988; Birks, 1995) by detrended canonical correspondence analysis (DCCA; ter Braak, 1986). The gradient length of DCCA axis 1 is a measure of compositional change in the diatom data in standard deviation (S.D.) units along the pH gradient (ter Braak & Juggins, 1993; Birks, 1995). The statistical significance of the pH-diatom relationship was assessed by

Table 1. Calibration data-set characteristics

	Minimum	Maximum	Mean	Median	S.D.
Environmental variable					
pH (units)	4.16	8	6.31	6.39	0.74
Diatom					
presence (taxa/lake)	8	31	17.66	17	5.83
taxa occurrences in data-set	1	49	6.35	3	8.3

Table 2. Type of taxon responses to pH, their WA optimum, WA tolerance and number of occurences. Only taxa that occur in 5 or more lakes were considered (in total 82 taxa)

Type of response	Taxa	Optimum	Tolerance	Occurrence
Unimodal asymmetric	*Aulacoseira distans nivaloides*	5.97	0.64	11
	Aulacoseira distans tenella	6.16	0.83	33
	Cyclotella bodanica lemanica	6.62	0.52	36
	Cyclotella michiganiana	7.07	0.69	7
	Cyclotella stelligera	6.49	0.56	38
	Cymbella gaeumanii	5.62	0.62	10
	Cymbella hebridica	5.17	1.06	9
	Eunotia bilunaris	5.19	0.96	11
	Eunotia exigua	5.92	0.86	8
	Eunotia pectinalis ventralis	5.18	0.89	8
	Eunotia rhomboides	4.84	0.39	8
	Fragilaria brevistriata (form3)	6.67	0.16	9
	Fragilaria fasciculata	5.73	0.78	6
	Fragilaria virescens exigua	5.89	0.59	15
	Navicula radiosa	6.71	0.62	11
	Navicula subtillissima	5.4	0.52	12
	Neidium ampliatum	5.09	0.74	12
	Neidium iridis	5.04	1.02	9
	Tabellaria(form1)	5.96	0.7	11
Unimodal symmetric	*Amphicampa hemicyclus*	5.58	0.63	6
	Asterionella formosa	6.08	0.74	41
	Aulacoseira alpigena	6.47	0.41	17
	Aulacoseira italica subarctica	6.51	0.4	38
	Brachysira brebissonii (form1)	6.07	0.51	33
	Cyclotella comensis	6.39	0.4	8
	Cyclotella ocellata	6.73	0.32	11
	Cyclotella pseudostelligera (form3)	7.06	0.45	5
	Cymbella gracillis	6.17	0.53	10
	Eunotia bidentula	4.66	0.35	7
	Eunotia incisa	6.13	0.48	20
	Eunotia pectinalis	6.38	0.35	9
	Fragilaria intermedia	7.24	0.36	5
	Fragilaria pinnata pinata	7.19	0.46	10
	Frustulia rhomboides var. saxonica	6.28	0.35	24
	Navicula mediocris	6.11	0.41	5
	Tabellaria flocculosa (form3)	6.29	0.54	49
	Tabellaria flocculosa (form4)	4.97	0.3	7
	Tabellaria fenestrata	6.46	0.32	22
	Tabellaria quadrisepta	6.29	0.33	9
	Tabellaria ventricosa	6.37	0.15	10
Sigmoid increasing	*Achnanthes minutissima minutissima*	6.71	0.99	42
	Amphora ovalis	6.79	0.42	7
	Brachysira vitrea	6.78	0.95	14
	Eunotia tenella	6.74	0.6	16
	Fragilaria brevistriata (form1)	6.73	0.78	7
	Fragilaria construens binodis	6.88	0.86	17
	Fragilaria construens venter	7.04	1.06	14
	Fragilaria lata	6.65	1.16	10
	Gomphonema gracile	6.77	0.61	7
	Navicula pupula pupula	6.73	0.61	10
Sigmoid decreasing	*Actinella punctata*	5.2	0.92	6
	Aulacoseira nygaardii	5.32	0.98	6
	Aulacoseira perglabra	5.32	1.97	16

Table 2. Continued

Type of response	Taxa	Optimum	Tolerance	Occurrence
	Eunotia faba	5.85	0.94	7
	Frustulia rhomboides	5.47	1.02	25
	Pinnularia braunii	5.3	1.34	15
	Pinnularia gibba	5.81	1.02	14
	Pinnularia microstauron (form1)	5.84	1.15	6
	Pinnularia microstauron (form2)	5.63	0.76	11
	Stauroneis agrestis	5.7	1.03	6
	Tabellaria ventricosa	5.78	0.93	24
No relation	*Aulacoseira ambigua*	6.47	1.07	11
	Aulacoseira distans distans	6.53	0.92	22
	Aulacoseira distans humilis	6.34	0.65	14
	Aulacoseira lirata	6.2	0.67	25
	Brachysira brebissonii (form3)	5.88	0.47	5
	Cyclotella meneghiniana	6.69	0.56	5
	Cyclotella pseudostelligera (form1)	6.32	0.75	8
	Cymbella incisa	6.38	0.44	5
	Cymbella microcephala	6.53	1.46	8
	Cymbella silesiaca	6.3	0.46	9
	Eunotia bilunaris mucophyla	6.01	0.69	19
	Eunotia paludosa	6.43	0.73	8
	Eunotia polyglyphis	6.67	1.19	6
	Eunotia subarcuatoides	5.99	0.65	6
	Fragilaria nanana	6.471	0.81	5
	Navicula subatomoides	6.5	0.84	9
	Navicula laevissima	6.45	0.9	9
	Nitzschia fonticola	6.35	1.18	8
	Nitzischia minutula	6.46	0.68	12
	Pinnularia maior	6.49	0.58	8
	Stauroneis phoenicenteron	6.04	1.13	10

Monte Carlo permutation tests involving 99 unrestricted permutations (ter Braak, 1990). DCCA was implemented using CANOCO version 3.12 (ter Braak, 1988, 1990).

We also evaluated the relationship to pH of all taxa occurring in a least 5 lakes (82 taxa). The statistical relationship was assessed using a hierarchical set of taxon response models (Huissman et al., 1993). This hierarchical set of response models consists of a skewed asymmetric unimodal response model, a symmetric Gaussian unimodal response model (ter Braak & Looman, 1986; Birks et al., 1990), a monotonically increasing or decreasing sigmoidal response model (Birks et al., 1990), and a null model with no relationship to pH (Birks et al., 1990). The taxon response modelling was done using the program HOF (J. Oksanen, unpublished program). Taxa with statistically significant fits to pH under the different types of response models are given in Table 2.

WA and WA-PLS models

As the data-set had a gradient greater than 2.5 S.D units along its pH gradient, the unimodal techniques of Weighted Averaging (WA) and Weighted Averaging Partial Least Square (WA-PLS) were used to develop pH diatom-based inference models. In WA regression, the optimum for each taxon is estimated from the training set based on the abundance of diatoms in the surficial sediment and the measured environmental variables (Birks et al., 1990). The regression step then allows inference of the environmental conditions from the diatom composition (Birks et al., 1990). WA-PLS is an extension of simple WA (ter Braak & van Dam, 1989; Birks et al., 1990) in which successive components are extracted from the training set. WA and WA-PLS were carried out using a SAS/IML implementation of the algorithm (Y.T. Prairie, unpublished program). In this program, the final number of components retained in

the model corresponds to the minimum number of components whose jackknifed RMSE is not significantly (as assessed by an F ratio on the MSEs) higher than the model with the minimum $RMSE_{jackknife}$ (van der Voet, 1994).

ANN models

To compare with the WA and WA-PLS models, we used back-propagation neural networks with 3 layers. Each unit of the first layer (input) is an identity neuron. Their activity represents the values of the relative abundance (%) of the diatom species in a sample. The output layer is composed of a unique unit (linear activation function) representing pH. The hidden layer contains units with symetrical-sigmoid activation functions. The number of units in this layer depends on the complexity of the problem. In order to find the best possible network, we tried various numbers of hidden layer units (2, 3, 5, and 10). So-called bias neurons, connected to each neuron on the hidden layer and the output layer were also used. This type of neuron is similar to a constant in a multiple regression. The pH neural network models were built using YANNS (Yet Another Neural Network Simulator) (Boné et al., 1998).

Models validation

WA and WA-PLS

The predictive ability of these diatom-based calibration models was assessed by the coefficient of determination between the measured and the diatom-inferred values (R^2) and the apparent root mean square error (RMSE). However, $R^2_{jackknife}$ and $RMSE_{jackknife}$ were also computed as they are more realistic measures of predictive power than the apparent statistics (Birks, 1998). Jackknifing consists of an iterative re-sampling technique involving a new training set of n-1 lakes from the original calibration set and its application to the one excluded sample. Further aspects of the model performance are the average bias and the maximum bias in the residuals for the test set (ter Braak & Juggins., 1993). For estimation of maximum bias, the sampling interval was subdivided into 10 equal intervals, the bias per interval calculated and the maximum of the 10 values calculated (ter Braak & Juggins., 1993).

ANN

Given the relatively low number of lakes (76) in this study, usual cross-validation methods (K-fold cross-validation or Hold-out procedure (German et al., 1992)) were not appropriate. These methods consist of randomly dividing the calibration set into two subsets (learning and validation 1:1, 2:1 or 3:1, etc..) and are not well-suited to short and large data sets typical of paleolimnological applications. This is because the training set still has to be large enough to be representative and the validation set has to be large enough to allow a robust validation of the network. We therefore used the same validation method as used in WA and WA-PLS models, namely leave-one-out cross-validation or jackknifing cross-validation (Efron, 1983; Kohavi, 1995). In this case, each lake in the calibration data-set (species/environmental variables couplets) is successively used in the validation. The jackknifing technique consists of building a complete set of networks (each with n-1 training examples and 1 validation case) and attempts to find, for the entire set of networks, a common number of iterations for an optimal generalization. This generalization is expressed as the average $RMSE_{jackknife.}$ The number of iterations used in the construction of the final network uses the early stopping method, that is when the average error in the validation set is minimal. This avoids overfitting (overtraining). Apparent RMSE is given by the average error in the learning set when training is stopped. $RMSE_{jackknife}$ is given by the average error in the validation set. We also evaluated the average and the maximum bias of the residuals as previously described.

Results and discussion

Data-set characteristics

The diatom data-set is large (214 taxa × 76 lakes), sparse (8–31, mean = 18 taxa per sample, 91% of zero values) and can therefore be characterized as noisy. pH values are normally distributed in the data set (Shapiro-Wilk W statistic = 0.96, prob (W) = 0.06) and the range of the observed values is large (4.16–8.05 mean = 6.31). Fifty percent of samples in the data-set have a pH between 6 and 6.74. Only 5 lakes have a pH < 5 and 10 lakes a pH > 7. Table 1 shows the details of the calibration data-set characteristics.

Monte Carlo permutation tests of DCCA axis 1 constrained to pH show that the data-set has a statistically significant (F ratio = 3.45, p value = 0.01) relationship to pH. pH explains 4.5% of the variance in the data-set and the gradient length is 3.55 S.D.

Table 2 shows the type of response of all taxa present in 5 lakes or more (40% of total species). Seventy five

percent of these taxa have statistically significant responses to pH; 50% have a symmetric Gaussian or asymmetric unimodal responses while 25% have an increasing or decreasing sigmoidal response. Given the long gradient length (3.55 S.D., pH range of 3.86 units), it is surprising that only 50% of taxa have a unimodal response to pH.

ANN pH-inference models

Optimal performances were obtained with 3 units in the hidden layer (214/3/1) (Table 3). RMSE decreases exponentially as the number of training epochs (iterations) increases while $RMSE_{jackknife}$ decreases and then increases (Figure 2). The best pH model was obtained after 700 epochs (Figure 3). RMSE and $RMSE_{jackknife}$ were 0.24 and 0.45, respectively. The apparent coefficient of determination (R^2) was 0.9 while $R^2_{jackknife}$ was 0.63. Figures 3a and 3b illustrate the fit between the estimated or jackknifed-predicted and observed pH when RMSE and $RMSE_{jackknife}$ are minimal. Figures 3c and 3d illustrate the distribution and the homogeneity of residuals. Residuals are normally distributed (Shapiro-Wilk W test = 0.98 prob W ≈ 0.90) and the average bias and maximum bias are, respectively, 0.14 and 1.13 pH units. We did not observe any systematic trend in the residuals (Figure 3d).

WA and WA-PLS pH-inference models

WA pH-inference models gave an apparent and jackknifed RMSE of, respectively, 0.33 and 0.5 pH units, with corresponding apparent R^2 and $R^2_{jackknife}$ of 0.81 and 0.56. Other summary statistics are given in Table 3. Plots of observed pH against estimated (apparent) (Figure 4a), or jackknifed-predicted pH (Figure 4b), and their corresponding residual plots (Figures 4c & 4d) show that there is a systematic bias in the predictive model, with a tendency for predicted values to be over-estimated at low pH and under-estimated at high pH values. The range of predictions is almost 2 times smaller (5.17–7.26, 2.09 units) than the observed range (4.16–8.0, 3.84 units). This bias disappeared after inverse deshrinking (Birks et al., 1990).

Table 3. Descriptive ANN, WA and WA-PLS pH-models summaries

	ANN	WA	WA-PLS
Number of components		1	3
Number of hidden units (ANN)	3		
Number of samples used	76	76	76
Number of taxa used	214	214	214
Number of iterations (ANN)	700		
$RMSE_{apparent}$ (pH units)	0.24	0.33	0.23
$RMSE_{jackknife}$ (pH units)	0.45	0.5	0.48
$R^2_{apparent}$	0.9	0.81	0.9
$R^2_{jackknife}$	0.63	0.56	0.58
Mean bias	0.14	–0.09	–0.15
Max bias	1.13	–1.07	–1.08

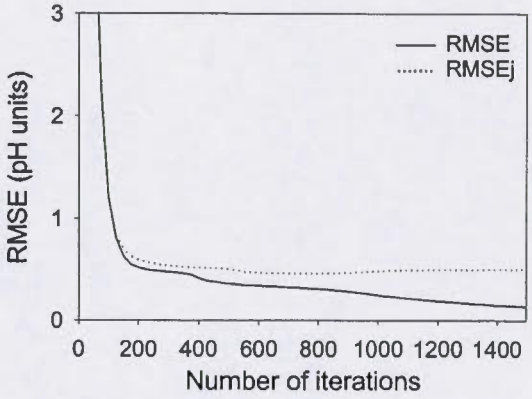

Figure 2. Changes in root-mean-square error of estimation (apparent RMSE) and root-mean-square error of prediction ($RMSE_{jackknife}$) for pH with increasing number of iterations in 3-layer back-propagation neural network with 3 units in the hidden layer. The netwoks were trained over 60 intervals of 25 iterations each (in total 1,500 iterations).

Three-component WA-PLS pH-inference models gave slightly better results than WA: 0.23 pH units for RMSE, 0.48 for $RMSE_{jackknife}$ while R^2 and $R^2_{jackknife}$ are 0.90 and 0.58, respectively (Table 3). Figures 5a and 5b show the fit between the observed and estimated pH values and the observed and jackknifed-predicted pH values. Mean bias and maximum bias are, in this case, –0.15 and –1.08 (Table 3). The WA-PLS model out-performs the WA model mainly because the high pH values are not underestimated (Figure 5d). In this case, the predicted range (4.64–8.19, 3.55 units) is almost as large as the observed range. Because the number of components of the final WA-PLS model is chosen on the basis of the decreasing RMSE with successive components before deshrinking, it is quite conceivable that the secondary components of any WA-PLS models serve mostly as a deshrinking component. Contrary to ANN models, the residuals from the WA and WA-PLS models were not normally distributed (Figures 4c & 5c).

Taxon inclusion in the models

How many taxa to include in an inference model has already been addressed to some extent by Birks (1994)

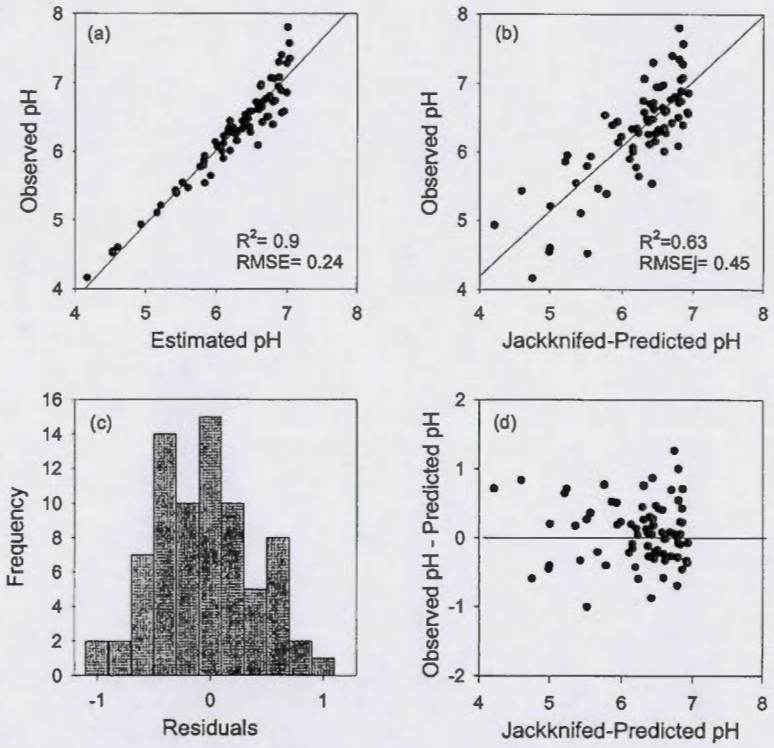

Figure 3. (a) Plot of observed pH values for the 76 lakes within the calibration set against estimated pH values. The estimated values are based on the training set of a 3-layer back-propagation network with three units in the hidden layer. (b) Plot of observed pH values against jackknifed-predicted pH values. The jackknifed-predicted values are based on the validation set (leave-one-out). For (a) and (b), the fitted line is based on Model I regression. (c) Diagram of the distribution of the residuals (from b). (d) Plot of residuals (from b) against predicted pH.

and Wilson et al. (1996). Inclusion criteria can be based either on a minimum abundance limit (i.e., 1% relative abundance) or based on the occurrence of the taxa in a minimum number of samples. Here we present an analysis based on the taxon's tolerances calculated prior to the development of the models. A series of numerical experiments was done to see if deletion based on tolerance resulted in any change in WA-PLS and ANN performances. For this purpose, only taxa that occur in 5 or more lakes were considered.

As a high tolerance is indicative of ubiquitous taxa and therefore unlikely to be affected by environmental changes, we successively deleted from the data matrix taxa with the highest tolerances (0.9, 0.8, . . ., 0.5). For the ANN models, this procedure led to a slight reduction in performance (as revealed by the $R^2_{jackknife}$, Figure 6a) but, overall, the ANN performance remained very stable. This was not the case for WA-PLS models, where the performance steadily improved as taxa with high tolerances were removed. Ultimately, the best fit was achieved when taxa with tolerances above 0.6 pH units were omitted ($RMSE_{jackknife}$ = 0.40 pH units and $R^2_{jackknife}$ = 0.72). It is interesting to note that the taxa with a high tolerance are essentially the taxa with a sigmoidal response curve as opposed to a unimodal response, as WA-PLS assumes.

We then evaluated in the same general manner whether the deletion of taxa with narrow tolerances would affect the predictive capacities of the WA-PLS and ANN models. Although not biologically surprising, our results show that the removal of non-ubiquitous taxa (e.g., taxa with a unimodal response curve) greatly affected the predictive power of WA-PLS models (Figure 6b). However, this procedure hardly affected the performance of the ANN model (Figure 6b). These results demonstrate that, unlike WA-PLS inference models, it is possible for ANN to infer pH from taxa with a high tolerance. Clearly, the taxa information used by the ANN is substantially different, both numerically and conceptually, from that used by WA-PLS.

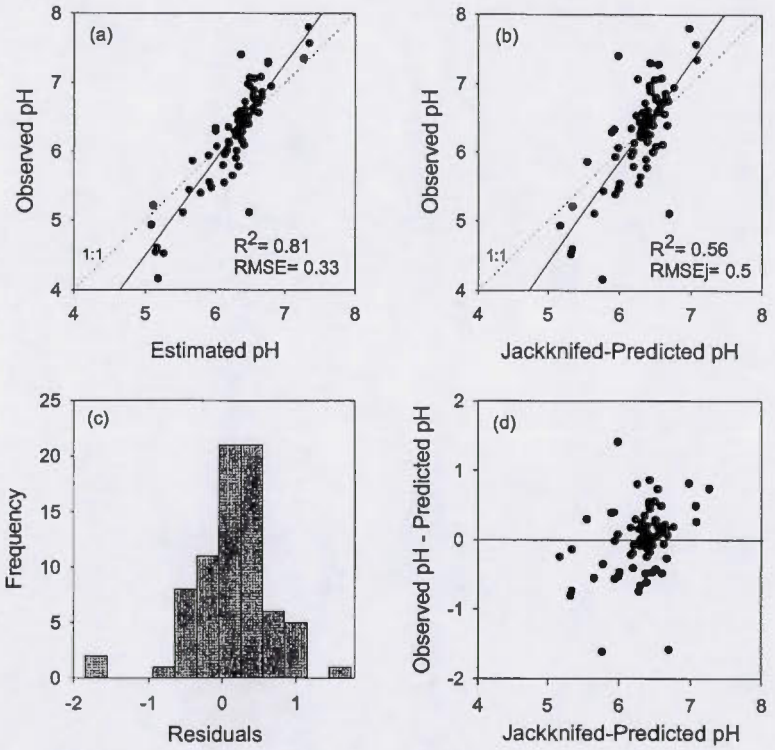

Figure 4. (a) Plot of observed pH values for the 76 lakes within the calibration set against estimated pH values. The estimated values are based on weighted averaging (WA) regression. (b) Plot of observed pH values against jackknifed-predicted pH values. The jackknifed-predicted values are based on a leave-one-out. For (a) and (b), the fitted line is based on Model I regression. (c) Diagram of the distribution of the residuals (from b). (d) Plot of residuals (from b) against predicted pH.

Comparison of the models

It is important to note that the WA-PLS and ANN models differ in two major ways. First, contrary to WA-PLS models, ANNs do not require that taxa show a unimodal relation to pH to obtain good results. In fact, the inclusion or exclusion of taxa depending on their tolerance indicates that the WA-PLS performance depends largely on the percentage of low-tolerance taxa within the calibration set. Second, even if the results show that the predictive abilities of WA-PLS and ANN models are relatively similar in global terms such as $RMSE_{jackknife}$ or $R^2_{jackknife}$ when all taxa are used, we observed that the predictions for a given lake can be very different between the two predictive models. Figure 7 illustrates the similarities and differences between the two models as a plot of ANN predictions vs. WA-PLS predictions. Predicted pH can differ by nearly one pH unit for some lakes depending on the model used. The average absolute difference between the models' predictions was 0.30 pH unit.

This reinforces the notion that the two types of models are not only different mathematically, they are also different in the taxon information used in their prediction. They should therefore be viewed as complementary models. This is further demonstrated by the fact that the model based on the average prediction of the two models is better ($R^2_{jackknife}$ = 0.74, $RMSE_{jackknife}$ = 0.38, mean bias = 0.005, and maximum bias = –0.71) than either of the models alone (Figure 8). When we combined the predictions obtained from the best WA-PLS model (with wide-tolerance taxa removed) with the best ANN model, the predictions were again improved. Clearly, the information extracted from the diatom assemblage data is not implemented in the same way by the WA-PLS and ANN algorithms. It suggests that each model is capable of capturing a part, but not all, of the underlying complex relationships between diatom assemblages and pH. If this is the case, the development of dual models, based on the average re-

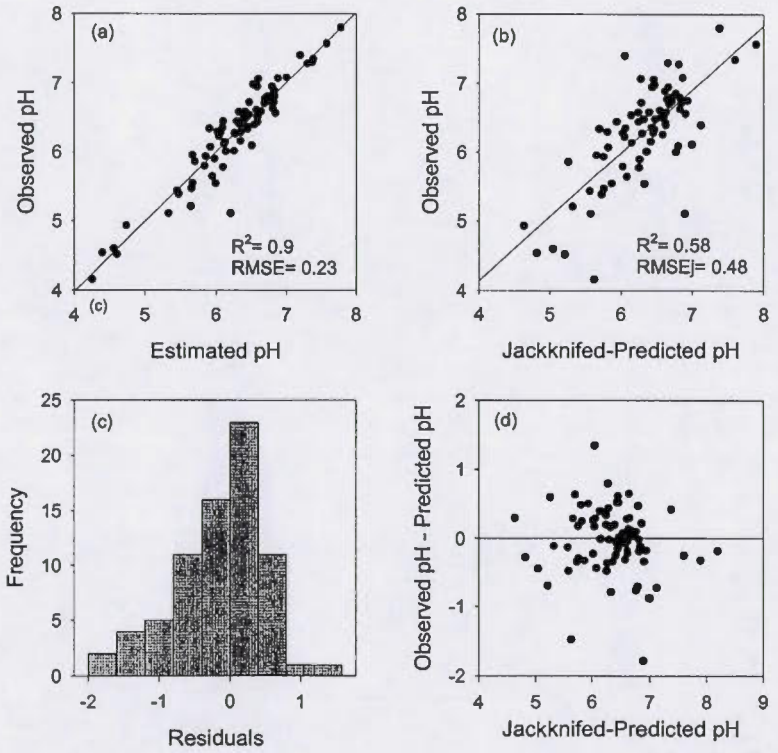

Figure 5. (a) Plot of observed pH values for the 76 lakes within the calibration set against estimated pH values. The estimated values are based on a three-component weighted averaging partial least square (WA-PLS) regression. (b) Plot of observed pH values against jacknifed-predicted pH values. The jacknifed-predicted values are based on a leave-one-out. For (a) and (b), the fitted line is based on Model I regression. (c) Diagram of the distribution of the residuals (from b). (d) Plot of residuals (from b) against predicted pH.

sults of both WA-PLS and ANN, may become a tedious but necessary procedure to obtain more reliable and robust reconstructions. The next step will be to compare results of this multi-model approach to those obtained from the increasingly popular, but even more tedious, multi-proxy models (Lotter et al., 1998). We

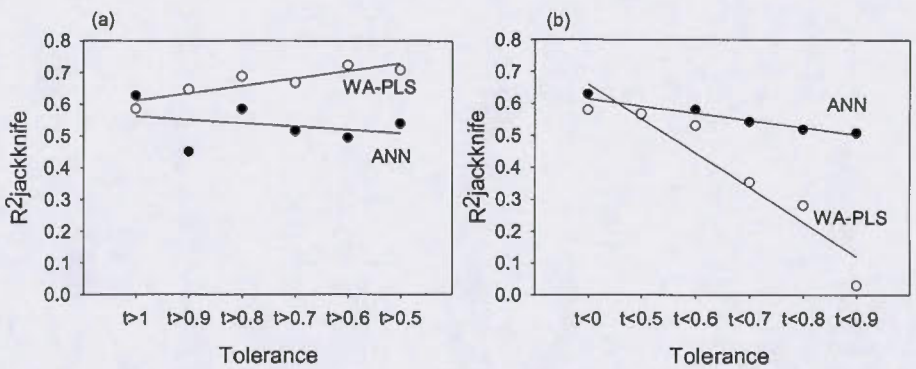

Figure 6. Plots illustrating the changes of $R^2_{jackknife}$ (a) when taxa with high tolerance are progressively removed (0.9, 0.8, . . ., 0.5 pH units) and (b) when taxa with low tolerance (0.5–0.9) are progressively removed.

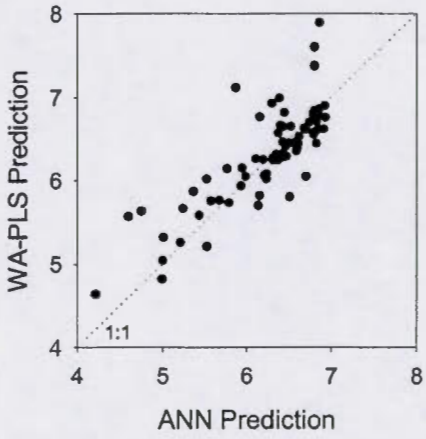

Figure 7. Plots illustrating the differences between ANN and WA-PLS predictions for each lake in the calibration data-set.

are presently attempting to generalize our results to the prediction of variables other than pH.

Conclusion

In this paper, we introduced the application of ANNs to paleolimnological pH reconstruction based on diatoms. Our comparison of the relative performance of WA-PLS and a three-layer back-propagation network models on a pH-diatom data-set from 76 lakes showed that Artificial Neural Networks can provide reliable paleolimnological inference models and that their predictive power is similar to that obtained from WA-PLS. However, they also differed on a number of points. WA-PLS is much more sensitive to taxon deletion based on their tolerance levels than ANNs. The two types of models appear to differ in the way information is extracted from the biological data and, as a result, they are complementary. Dual models produced the best predictive models.

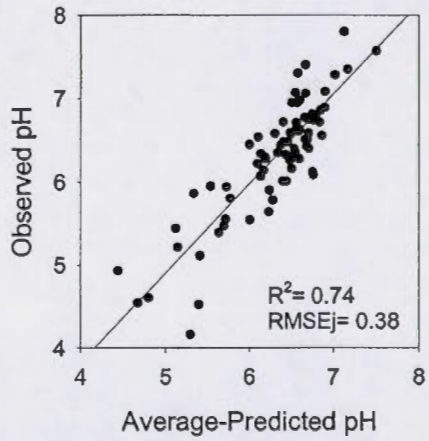

Figure 8. Plot of observed pH values for the 76 lakes within the calibration set against average-predicted pH values. The predicted values are based on the average prediction of the two models (WA-PLS and the 3-layered back-propagation networks) when all taxa are used. The fitted line is based on Model I regression.

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Appendix

A brief algorithm of back-propagation in neural networks. Adapted from Lek et al. (1996).

1. Initialize the number of hidden nodes.
2. Initialize the maximum number of iterations and the learning rate (η). Set all weights to small random numbers.
3. For each training vector (input $X_p = (x_1, x_2, \ldots x_n)$, output Y) repeat steps 4–7.
4. Present the input vector to the input nodes and the output to the output node.
5. Calculate the input to the hidden (h) nodes:

$$a_j^h = \sum_{i=1}^{n} W_{ij}^h \cdot x_i \qquad (1)$$

with a_j: activation of the jth downstream neuron, x_i: value at the outlet of the ith neuron of the first layer (relative abundance of taxon i), W_{ij}: weight of the connection between the ith neuron of the first layer and jth neuron of the hidden layer

Calculate the output from the hidden nodes:

$$x_j^h = f(a_j^h) = \frac{\exp(a_j^h) - 1}{\exp(a_j^h) + 1} \qquad (2)$$

Calculate the input to the output (k) node:

$$a_k = \sum_{j=1}^{L} W_{jk} \cdot x_j^h \text{ (with } L\text{: number of hidden nodes)} \qquad (3)$$

and the corresponding output:

$$\hat{Y}_k = f(a_k) = a_k \text{ (notice that in our case } k=1 \text{ and } \hat{Y}_k = \hat{Y}) \quad (4)$$

6. Calculate the error term for the output node:

$$\delta_k = (Y - \hat{Y}) \quad (5)$$

and for the hidden nodes:

$$\delta_j^h = f'(a_j^h) \sum_k \delta_k W_{jk} \quad (6)$$

7. Update weights on the output layer:

$$W_{jk}(t+1) = W_{jk}(t) + \eta \delta_k x_j^h \quad (7)$$

and the hidden layer:

$$W_{ij}(t+1) = W_{ij}(t) + \eta \delta_j^h x_i \quad (8)$$

While network errors are larger than some preferred limit or the number of iterations is smaller than the maximum number of iterations, repeat steps 4–7.

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